HARVARD UNIVERSITY

Ernst Mayr Library
of the Museum of
Comparative Zoology

TULANE STUDIES IN
ZOOLOGY AND BOTANY

MCZ
LIBRARY

DEC 0 2 1991

HARVARD
UNIVERSITY

Volume 28, Number 1 1991

ETHEOSTOMA TALLAPOOSAE AND *E. BREVIROSTRUM*, TWO NEW DARTERS, SUBGENUS *ULOCENTRA*, FROM THE ALABAMA RIVER DRAINAGE

ROYAL D. SUTTKUS
MUSEUM OF NATURAL HISTORY, TULANE UNIVERSITY
BELLE CHASSE, LOUISIANA 70037

AND

DAVID A. ETNIER
DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TENNESSEE
KNOXVILLE, TN 37996

Tulane
University
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY AND BOTANY

ISSN 0082-6782

Department of Ecology, Evolution, and Organismal Biology
Tulane University, New Orleans, Louisiana, 70118

INFORMATION FOR AUTHORS

Manuscripts dealing with all aspects of ecology, evolution, and systematic biology are encouraged. All manuscripts are reviewed.

Page charges are assessed at the rate of $45 per page. Some limited financial assistance from the George Meade Memorial Fund is available if authors are unable to meet these charges.

Style of manuscript should follow guidelines appearing in the Council of Biology Editors Style Manual.

Manuscript (with abstract) must be typed on good quality 8.5 x 11 inch paper, double-spaced throughout (including Literature Cited, figure captions, footnotes, and tables). All pages must have 1 inch margins on all sides. Dot-matrix printing is not acceptable; do not justify right-hand margins. Do not hyphenate words at ends of lines. Last name(s) of author(s) should appear on each page with page number; this includes tables and figure captions.

Lettering used in figures must be easily read after reduction to our page size. Photographs (halftones) should be made for no or little reduction.

The original and three copies of the manuscript, along with figures, should be submitted.

Prospective authors should request a copy of the detailed guidelines for manuscript preparation (including footnotes, typefaces, literature and specimen citation, and dimensions of figures) from the Editor at the above address.

EXCHANGES AND SUBSCRIPTIONS

Tuland Studies in Zoology and Botany is available for exchange with institutions publishing comparable series. Otherwise, standing orders are accepted, with issues priced individually (foreign postage extra). A price list for back issues is available on request. Remittances should be made payable to Tulane University.

Etheostoma tallapoosae and *E. brevirostrum*, two new darters, subgenus *Ulocentra*, from the Alabama River drainage

Royal D. Suttkus
Museum of Natural History, Tulane University
Belle Chasse, LA 70037

David A. Etnier
Department of Zoology, University of Tennessee
Knoxville, TN 37996

Abstract

Etheostoma tallapoosae and *E. brevirostrum*, two new darters, subgenus *Ulocentra*, are described from the Mobile basin. *Etheostoma tallapoosae* is confined to the Tallapoosa River system of Alabama and Georgia, and it is the only species of *Ulocentra* in that system. It lacks a red ocellus in the spinous dorsal fin and has additional coloration suggesting that its affinities are with the several undescribed *Ulocentra* occurring on the Gulf Coastal Plain. *Etheostoma brevirostrum* is confined to the upper Coosa River system of Alabama, Georgia, and Tennessee, where it is occasionally sympatric with *E.* (*Ulocentra*) *coosae* and narrowly allopatric from an undescribed *Ulocentra* that occurs in tributaries to the middle portion of the Etowah River. *Etheostoma brevirostrum* males are unique among *Ulocentra* in having red blotches surrounded by white or yellow on the lower side, and they uniquely share a median red band in the anal fin with *E. etnieri* of middle Tennessee and *E. pyrrhogaster* of northwestern Tennessee and southwestern Kentucky. *Etheostoma tallapoosae* has a small geographic distribution, but is locally abundant. *Etheostoma brevirostrum* is an uncommon species, known from few localities, and warrants consideration for protected status.

Introduction

The subgenus *Ulocentra* sensu Bouchard (1977) and Bailey and Etnier (1988) contains ten described species and four or five undescribed species in addition to the two species described here. Members of this subgenus, commonly called the snubnose darters, occur in Gulf Coastal drainages east of the Mississippi River, several eastern tributaries to the lower Mississippi River, the Tennessee and Cumberland River drainages, and southern tributaries to the Ohio River. They are absent from Atlantic slope drainages and the area west of the Mississippi River. In addition to the above papers, which include descriptions of three new species of *Ulocentra*, Page and Burr (1982) described three *Ulocentra* species from the Cumberland and Ohio River drainages, and Etnier and Bailey (1989) described an additional species shared by the Cumberland and Tennessee River drainages. Thus, seven of the ten recognized nominal species in the subgenus have been described since 1977.

Snubnose darters are typically inhabitants of flowing pools and gentle riffle areas in small streams, where they are often very common. They are small– to

moderate–sized darters, not known to exceed 70 mm standard length. Males of most species maintain considerable red and orange color throughout the year, these intensifying and blue and green colors often appearing during the early spring breeding period. During each spawning act, the female, accompanied by a male, attaches 1 egg to a hard surface, typically the side of a large rock (O'Neil, 1981; Page and Mayden, 1981; Stiles et al., 1987; Carney and Burr, 1989).

The two darters described here have been known for about three decades, but their distribution and taxonomic status relative to other *Ulocentra* species of the Gulf Coast were unclear. The Tallapoosa darter, *Etheostoma tallapoosae*, is the sole representative of the subgenus *Ulocentra* in the Tallapoosa River system, but the holiday darter, *Etheostoma brevirostrum*, occurs sympatrically with the Coosa darter, *Etheostoma coosae*, in part of the Coosa River system. There is yet another snubnose darter that occurs in the middle section of the Etowah River system, mostly upstream from *E. coosae* populations there, and isolated from *E. brevirostrum* populations that are in the extreme upper part of the Etowah system. Additional undescribed species of *Ulocentra* occur in the Alabama River drainage below the confluence of the Tallapoosa and Coosa rivers, in other parts of the Mobile basin, in drainages east of Mobile basin through the Choctawhatchee River, and in the Yazoo River system of northwestern Mississippi.

Materials and Methods

Specimens of the new species and comparative material of *Etheostoma coosae* are from the collections at Auburn University (AUM), Cornell University (CU), Tulane University (TU), University of Alabama (UAIC), University of Georgia (UGAMNH), and University of Tennessee (UT). In the listing of type material, each catalog number is followed by the number of specimens seen and range of standard length (SL) in millimeters, e.g., (10, 25–48). In addition to standard compass directions (with the following "of" deleted), the following abbreviations are used: Cr. = Creek, R. = River, mi = mile(s), airmi = airmile(s), trib. = tributary, Hwy = Highway, Rd. = Road, Co. = County, T = Township, R = Range, Sec = Section. In lists of materials not designated as types, the catalog number is followed by the number of specimens seen, enclosed in parentheses. We include collection dates for all of the holiday darter material because of the scarcity of collection sites and the fact that the species has disappeared from some localities in the southern part of its known range.

Counts and measurements were made as described in Hubbs and Lagler (1958) except as follows. Transverse body scales were counted from the origin of the anal fin diagonally upward to the base of the spinous dorsal fin. Gill rakers, counted on the anterior arch on either the left or the right side, include both dorsal and ventral rudiments. Measurements were made with needle-point dial calipers and recorded to the nearest 0.1 mm. Trans-pelvic width was measured between the outer bases of the pelvic spines.

Names used for associated fish species follow Robins et al. (1980), as we have yet to see and consider the many name changes anticipated in the forthcoming edition of the List of common and scientific names of fishes from the United States and Canada. We continue to refer to the widespread stoneroller of the Mobile basin as *Campostoma anomalum*, and not as *C. oligolepis* as suggested by

Burr and Cashner (1983), since preliminary studies by one of us (D.A.E.) indicate that the same stoneroller taxon present in the Ohio River drainage (type locality for *C. anomalum*) occurs throughout the Cumberland and Tennessee River drainages and most of the Mobile basin.

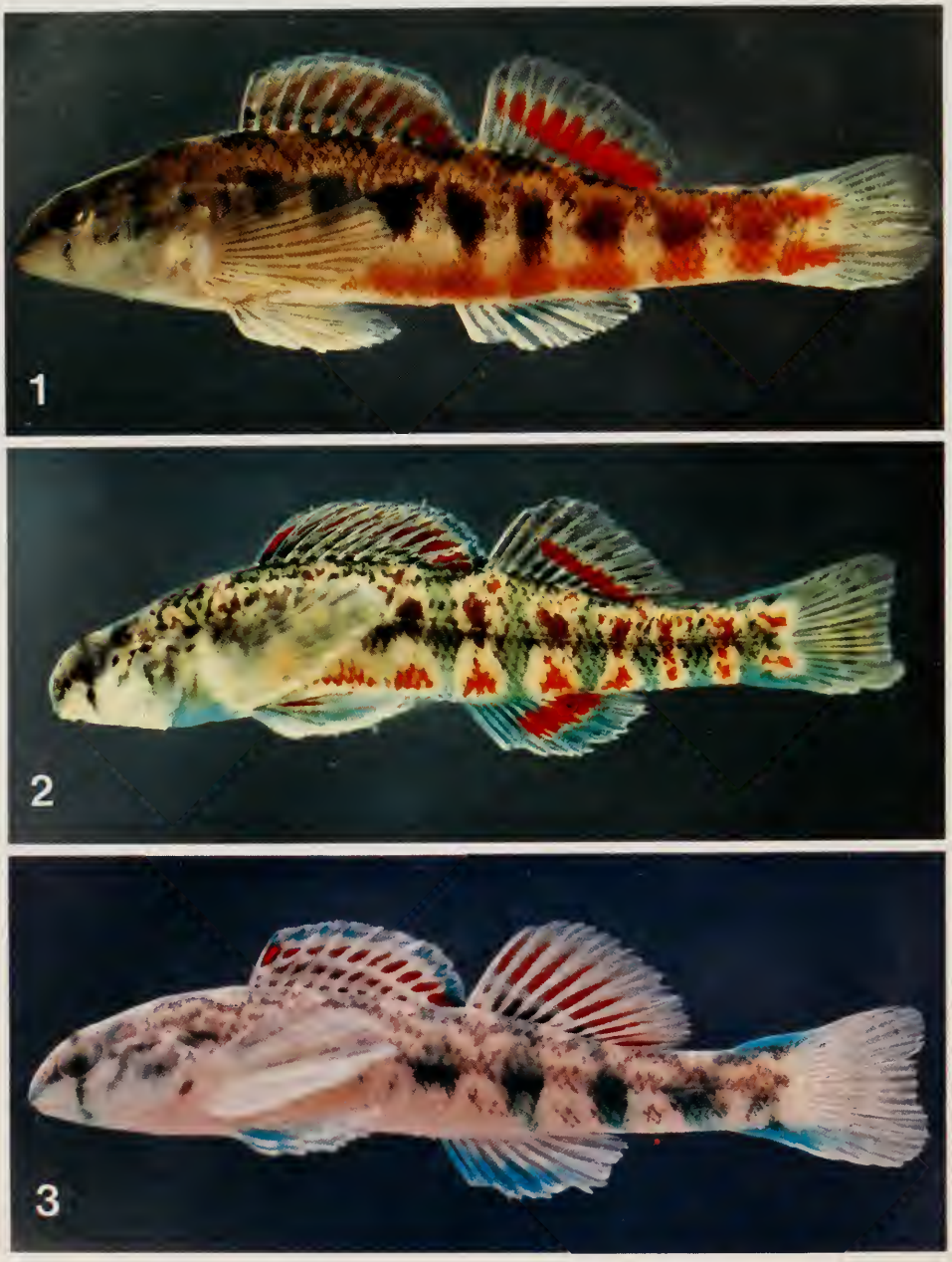
Etheostoma tallapoosae, new species
Tallapoosa Darter
Figures 1 and 4

Etheostoma (*Ulocentra*) sp. Jenkins, 1976 (undescribed species, distribution).
Etheostoma sp. Kuehne and Barbour, 1983: 99, *pl. 13* ("Tallapoosa snubnose darter," characterized, range map).
Tallapoosa darter. Page, 1983: *pl. 16E, 16F.*

HOLOTYPE: Adult male, TU 158215, 55.0 mm standard length, Gold Branch, tributary to Channahatchee Creek at Ala Hwy 63, 6 mi N of Eclectic (T20N, R21E, Sec 29), Elmore County, Ala, 16 March 1957, R. D. Suttkus, Rudolph J. and Helen V. Miller, and John DeAbate.

PARATOPOTYPES: TU 15275 (136, 30-55), collected with holotype are distributed as follows: TU 15275 (92), ANSP 167316 (4), AUM 25935 (4), CU 72359 (4), INHS 59305 (4), SIUC 18163 (4), UAIC 10016.01 (4), UF 84454 (4), UGAMNH 2167 (4), UMMZ 218251 (4), USNM 314352 (4), and UT 91.3925 (4); TU 12084 (4, 35-44), 5 October 1955; TU 41116 (45, 35-52), 12 April 1966; TU 152230 (7, 35-48), 14 May 1988; UT 91.3537 (13, 49-64), 12 March 1989; TU 157633 (11, 28-56), 23 March 1990; and TU 157803 (4, 48-55), 12 April 1990. Additional paratypes from Gold Branch at Elmore Co. Rd. 357, 1.7 mi SE Ala Hwy 63, Jordan, T20N, R21E, Sec 29, Elmore Co.: TU 152243 (15, 35-51), 14 May 1988; TU 157646 (18, 36-61), 23 March 1990; and TU 157793 (19, 30-51), 12 April 1990.

OTHER PARATYPES: TALLAPOOSA RIVER SYSTEM, ALABAMA. ELMORE COUNTY: TU 41137, (3, 32-36), Channahatchee Cr., 2.5 mi S Red Hill, T19N, R21E, Sec 10; UAIC 9700.10 (1, 51), Channahatchee Cr., 2.3 mi N Eclectic, Ala Hwy 63, T20N, R20E, Sec 35; UAIC 1363.10 (2, 43-47), trib. to Stearns Cr., 1.3 mi E Ala Hwy 9, 1.8 mi S Semen, T20N, R20E, Sec 17. COOSA COUNTY: UAIC 1359.15 (7, 23-39) and TU 158249 (8, 37-44), Okachoy Cr., 5.8 mi NE Equality, Ala Hwy 259, T21N, R20E, Sec 2. TALLAPOOSA COUNTY: AUM 2410 (1, 35), Saugahatchee Cr., 2.4 mi N Reeltown, Ala Hwy 49, T19N, R22E, Sec 13; AUM 16432 (1, 39), Blue Cr., 6.6 mi SSW Camp Hill, Ala Hwy 50, T20N, R23E, Sec 13; UT 91.1980 (7, 31-49), unnamed trib. to South Sandy Cr., 1 mi N US Hwy 280, 3.7 mi SE junction Hwy 280 and Co. Rd. 89, T21N, R24E, Sec 28; UAIC 1486.10 (4, 38-49), Manoy Cr. just E Jackson Gap, US Hwy 280, T22N, R22E, Sec 24; UAIC 9701.10 (25, 25-50), Elkahatchee Cr., 3.3 mi SW Alexander City, T22N, R21E, Sec 7; AUM 16413 (1, 42) and UAIC 1040.11 (2, 39-41), Hillabee Cr., 6.2 airmi NE Alexander City, Ala Hwy 22, T23N, R22E, Sec 16; AUM 16814 (20, 30-46) and TU (157616 (1, 41), Josie Leg Cr., trib. to Hillabee Cr., 6.6 airmi NE Alexander City, Ala Hwy 22, T23N, R22E, Sec 9; UAIC 1542.06 (8, 28-43), Hackney Cr., 1 mi S Hackneyville, Ala Hwy 63, T24N,



Figures 1–3. *Etheostoma* species from Alabama. 1. *E. tallapoosae*, TU 157803, paratype, adult male, 55 mm SL. Gold Branch, tributary to Channahatchee Creek, at Alabama Hwy 63, 6.0 miles north of Eclectic (T20N, R21E, Sec 29), Elmore County, Alabama, 12 April 1990, R. D. Suttkus and J. M. Pierson. 2. *E. brevirostrum*, TU 158216, holotype, adult male, 41 mm SL. Shoal Creek, tributary to Choccolocco Creek at Pine Glen Recreation Area, 8.1 miles north of US Hwy 78 (T15S, R10E, Sec 16), Cleburne County, Alabama, 10 May 1989, R. D. Suttkus and J. M. Pierson. 3. *E. coosae*, AUM 25941, male, 45 mm SL. East Fork Hatchet Creek at Coleta (T20S, R6E, Sec 21), Clay County, Alabama, 15 April 1989, J. M. Pierson. Photographs by J. M. Pierson.

R21E, Sec 23; UAIC 8473.13 (1, 28), Little Hillabee Cr., 2.3 mi ENE Hackneyville, T24N, R22E, Sec 7; UAIC 9348.11 (3, 19-53), Enitachopco Cr., 5.8 mi NW New Site at gravel road, T24N, R22E, Sec 3; UAIC 1523.02 (8, 39-40), Timbergut Cr., W New Site, Ala Hwy 22, T24N, R23E, Sec 31. CLAY COUNTY: UAIC 1543.06 (2, 30-41), unnamed trib. to Little Hillabee Cr., 5.1 mi N Hackneyville, T22S, R7E, Sec 10; UAIC 1038.12 (15, 27-44) and TU 41160 (12, 33-45), Little Hillabee Cr., 1.0 mi SW Millerville, Ala Hwy 9, T21S, R7E, Sec 20; UAIC 9311.14 (10, 39-58), Enitachopco Cr., 5.7 mi ESE Millerville at gravel road, T21S, R8E, Sec 32; AUM 16418 (4, 35-54), Enitachopco Cr., 3.8 airmi SSE Ashland, T21S, R8E, Sec 7; UAIC 1039.08 (28, 28-57), TU 29891 (30, 33-56), TU 32737 (21, 38-59), TU 40656 (57, 35-61), UAIC 2152.07 (3, 44-57), UAIC 3020.05 (2, 48-49), UAIC 8445.06 (4, 42-54), and TU 157781 (2, 42-54), Enitachopco Cr., 2.9 mi SW Ashland, Ala Hwy 9, T20S, R8E, Sec 31; AUM 19608 (3, 24-46), Enitachopco Cr., 2.1 airmi SW Ashland, Co. Rd. 34, T20S, R7E, Sec 25. LEE COUNTY: AUM 16399 (8, 32-51), Bird Cr., trib. to Saugahatchee Cr., 4.7 airmi N Loachapoka, T19N, R24E, Sec 2; AUM 20404 (1, 37), Loblockee Cr., Macon Mill, 3.7 airmi N Loachapoka, T19N, R25E, Sec 6; UAIC 1566.02 (2, 37-40), Macon Mill Cr. at Co. Rd. 11, N Loachapoka, T19N, R25E, Sec 2; AUM 15201 (2, 36-40), Little Loblockee Cr., 3.9 mi SE Waverly, US Hwy 280, T20N, R25E, Sec 23; UAIC 1529.11 (1, 29), trib. to Saugahatchee Cr., 0.6 mi SE Macon Mill, Co. Rd. 11, T19N, R25E, Sec 8. CHAMBERS COUNTY: AUM 20966 (32, 23-55), South Fork Sandy Cr., 2.8 mi ENE Waverly, T20N, R25E, Sec 11.

ADDITIONAL MATERIAL EXAMINED BUT NOT DESIGNATED AS TYPES: TALLAPOOSA RIVER SYSTEM, ALABAMA. TALLAPOOSA COUNTY: UAIC 7779.08 (4), UAIC 7780.10 (2), UAIC 7784.12 (10), UAIC 7791.11 (10), UAIC 7792.11 (5), UAIC 8486.21 (9), UAIC 8495.18 (3), UAIC 8499.11 (4), UAIC 8518.07 (2), UAIC 8523.11 (3), and UAIC 9274.11 (1), Emuckfaw Cr., 3.3 mi SSE New Site, Ala Hwy 49, T23N, R23E, Sec 9; AUM 22089 (15), Emuckfaw Cr., 5.5 airmi NE New Site, T24N, R24E, Sec 18; UAIC 1534.06 (1), Tallapoosa R., Ala Hwy 49, Horse Shoe Bend area, T23N, R23E, Sec 15; UAIC 9704.01 (11), Sweetwater Cr., 5.2 mi SW Daviston, T23N, R24E, Sec 7; AUM 13153 (23), Eagle or Jaybird Cr., 7.2 airmi SSE New Site, T23N, R23E, Sec 35; UAIC 8476.17 (4) and UAIC 9307.12 (1), Tallapoosa R., 6.7 mi SSW Daviston, T23N, R24E, Sec 19; UAIC 1522.05 (8), County Line Cr., S Hampton, between Hampton and Buttston, T23N, R24E, Sec 26. CHAMBERS COUNTY: UAIC 1521.07 (5), Allen Cr., 0.7 mi N Trammel Cross Rds., T23N, R25E, Sec 15; UAIC 9308.15 (2), Caty Cr., 0.5 mi SE Abanda, T24N, R25E, Sec 2; UAIC 7794.03 (1), UAIC 8475.12 (1), UAIC 8507.06 (4), UAIC 9284.15 (2), and UAIC 9305.11 (4), Tallapoosa R., 1.5 mi SSE Wadley, 1.6 mi W Abanda, T24N, R25E, Sec 4. RANDOLPH COUNTY: AUM 11203 (13), High Pine Cr., 1 mi S Dickert, T22S, R11E, Sec 11; UAIC 1378.09 (16), Jones Cr., trib. to High Pine Cr., 1 mi W Roanoke, US Hwy 431, T21S, R12E, Sec 22; UAIC 9247.18 (5), Beaverdam Cr., 1.0 mi NE Wadley at Co. Rd. 33, T22S, R10E, Sec 1; UAIC 1519.05 (17), Hurricane Cr., between Malone and Almond, T21S, R10E, Sec 27; UAIC 7781.05 (2), UAIC 8480.06 (3), UAIC 8497.02 (2), UAIC 8506.06 (2), UAIC 8508.12 (5), UAIC 8511.03 (3), UAIC 8520.03 (1), UAIC 9286.08 (3), UAIC 9292.06 (10), UAIC 9299.08 (2), and UAIC 9304.11 (5), Tallapoosa R., 4.0 mi NNW Wadley, T21S, R10E, Sec 26; UAIC 1518.11 (1), Cornhouse Cr., across Tallapoosa R. from Malone, at field road, T21S, R10E, Sec 11; UAIC 6793.20 (5), UAIC 7745.21 (15), UAIC 7746.11 (6), UAIC 7778.08 (11), UAIC 7788.04 (6), UAIC 7789.13 (2), UAIC 7790.11 (11), UAIC 7797.11 (8), UAIC 8487.13 (8), UAIC 8488.12 (5), UAIC 8489.15 (15), UAIC 8492.09 (17), UAIC 8493.13 (11), UAIC 8503.22 (9), UAIC 8505.11 (15), UAIC 9273.19 (9), UAIC 9277.18 (1), AUM 23297 (6), and AUM 23805 (9), Cornhouse Cr., 2.6 mi NE Malone, T21S, R10E, Sec 1; UT 91.2732 (3) and AUM 23923 (21), Cornhouse Cr. at Co. Rd., 6.6 airmi SSW Wedowee, T21S, R11E, Sec 6; UAIC 1379.11 (3), Cornhouse Cr., 7 mi NW Roanoke, US Hwy 431, T20S, R12E, Sec 31; UAIC 7744.15 (2), UAIC 7775.09 (1), UAIC 7795.14 (4), UAIC 7796.11 (2), UAIC 8483.08 (2), UAIC 8485.13 (2), UAIC 8487.13 (3), UAIC 8490.08 (4), UAIC 8496.10 (4), UAIC 8502.16 (2), UAIC 8504.15 (3), UAIC 8512.11 (2), UAIC 9276.23 (4), UAIC 9280.20 (3), UAIC 9301.18 (3), UAIC 9306.16 (6), and AUM 23793 (25), Crooked Cr., 4.6 mi NW Malone, T20S, R10E, Sec 31;

UAIC 9298.07 (4), Tallapoosa R., 4.6 mi SSE Ofelia near mouth of Crooked Cr., T20S, R10E, Sec 28; UAIC 1500.07 (3), Fox Cr., 7 mi E Lineville, Ala Hwy 48, T20S, R10E, Sec 6; UAIC 1506.07 (1), Tallapoosa R. at Fosters Bridge, W Milner, Co. Rd. 82, T19S, R10E, Sec 4; TU 56359 (5), Wedowee Cr., 1 mi NW Wedowee, US Hwy 431, T19S, R11E, Sec 34; TU 40671 (38) and AUM 13140 (6), Pineywood Cr., 2.9 mi W junction US Hwy 431 and Ala Hwy 82, 1 mi E Milner, T18S, R11E, Sec 31; UAIC 1497.09 (4), UAIC 9000.03 (7), and UT 91.2142 (10), Pineywood Cr., 11 mi NW Wedowee, US Hwy 431, T18S, R11E, Sec 29; UAIC 6278.08 (10) and UAIC 7163.01 (3), Pineywood Cr., Co. Rd. 19, 11.2 airmi NNW Wedowee, T18S, R11E, Sec 8; UAIC 8443.09 (3), Bear Cr., 3 mi W Woodland, Co. Rd. 97, T19S, R11E, Sec 12; UAIC 9197.07 (1), UAIC 1381.12 (3), and UT 91.1233 (4), Bear Cr., 2 mi SW Woodland, Ala Hwy 48, T19S, R12E, Sec 19; UAIC 6422.07 (2), Cane Cr., Ala Hwy 48, T19S, R12E, Sec 10; UAIC 1383.08 (31), Cohobadiah Cr., Co. Rd. 82, Newell, T18S, R12E, Sec 30; UAIC 6417.11 (14), Cutnose Cr., Ala Hwy 42, 4.0 airmi NNE Woodland, T18S, R12E, Sec 27; UAIC 9699.01 (1), Little Tallapoosa R., Meadow's Bridge, 2.0 mi ENE Newell, T18S, R12E, Sec 21; TU 158232 (1), Little Tallapoosa R., Thompson Bridge, 2.3 mi NW Graham, T18S, R12E, Sec 1. CLAY COUNTY: UAIC 1517.12 (12) and AUM 15033 (10), White Oak Cr., 1.2 mi S Cragford, T20S, R9E, Sec 35; AUM 14833 (3), AUM 14795 (3), and AUM 14881 (60), Wesobulga Cr., 2.5 airmi S Cragford, T21S, R9E, Sec 1; AUM 15743 (39) and UAIC 9310.16 (10), Wesobulga Cr., 4.5 airmi SSW Cragford, 0.7 mi W Corinth, T21S, R9E, Sec 16; UAIC 1036.09 (10), Crooked Cr. 2.3 mi S Lineville, Ala Hwy 48, T20S, R9E, Sec 19; UAIC 947.02 (1), Crooked Cr. 0.5 mi SW Lineville, Ala Hwy 48, T20S, R8E, Sec 12; UAIC 1508.09 (1), Little Ketchepedrakee Cr., 1 mi E Delta, Co. Rd. 47, T18S, R9E, Sec 25; UAIC 1501.07 (6), Ketchepedrakee Cr., 0.3 mi S Dempsey, T18S, R8E, Sec 23. CLEBURNE COUNTY: UAIC 1505.05 (7), trib. to Cohobadiah Cr. behind Rock Springs church, T17S, R11E, Sec 36; UAIC 1068.06 (15), Knakes Cr., 2 mi SW Hightower, Ala Hwy 46, T17S, R12E, Sec 20; UAIC 1069.10 (1) and AUM 16877 (1), Lockchelooge Cr., 0.5 mi E Tallapoosa R., US Hwy 431, T17S, R10E, Sec 32; UAIC 1504.08 (6), Lockchelooge Cr., 0.5 mi N Micaville, T17S, R10E, Sec 36; UT 91.2138 (11), trib. to Tallapoosa R. at Ala Hwy 9, W junction US Hwy 431, Hollis, T17S, R9E, Sec 25; UAIC 1503.07 (1), mouth of Dynne Cr., T17S, R10E, Sec 16; AUM 10055 (4), South Fork Dynne Cr., 8.2 airmi SSE Heflin, T17S, R10E, Sec 13; UAIC 1495.11 (4), Dynne Cr., 4 mi E Ala Hwy 9, Co. Rd. 19, T17S, R10E, Sec 2; UAIC 9290.11 (2), Tallapoosa R., 2.4 mi S Heflin, T16S, R10E, Sec 28; UAIC 1064.13 (5), Cahulga Cr., 0.2 mi W Heflin, US Hwy 78, T16S, R10E, Sec 17; UAIC 4501.01 (6), trib. to Cane Cr., 1 mi E Heflin, Ala Hwy 46, T16S, R10E, Sec 11; UAIC 1098.16 (13), Cane Cr., 2 mi E Edwardsville, US Hwy 78, T15S, R11E, Sec 11; UAIC 1066.10 (10), trib. to Tallapoosa R., 1.7 mi NW Tallapoosa R., Ala Hwy 46, T16S, R11E, Sec 16; UAIC 1067.07 (22), Verdin Cr., 3.2 mi E Tallapoosa R., Ala Hwy 46, T17S, R11E, Sec 3; UAIC 1319.11 (1), Kelly Cr., 0.5 mi N Lebanon, T15S, R12E, Sec 27; UAIC 1099.09 (9), Muscadine Cr., 1.3 mi E Fruithurst, US Hwy 78, T15S, R12E, Sec 5.

TALLAPOOSA RIVER SYSTEM, GEORGIA. CARROLL COUNTY: UAIC 1318.13 (2), Little Indian Cr., 5 mi N Bowdon, Co. Rd. S1813; UAIC 1307.07 (7), Juniper Cr., 1 mi E Ga Hwy 100, 8.8 mi S Tallapoosa; UAIC 1310.08 (14), Turkey Cr., 1 mi NW Mt. Zion, Co. Rd. S835; UAIC 1317.11 (5), Mountain Cr., 3 mi W Tyus, Ga Hwy 5; UAIC 1312.07 (1), Sharpe Cr., 4.5 mi N Carrollton, Ga Hwy 113. HARALSON COUNTY: UAIC 1309.09 (3), Walker Cr., 3.2 mi SW Waco, near Haralson/Carroll Co. line; UGAMNH 2054 (21), Mann Cr., Co. Rd. 165, 1.2 airmi WNW Poplar Springs; UGAMNH 2067 (16), Harris Cr., trib. to Beach Cr., 3.3 airmi WSW Buchanan, Co. Rd. 182; UGAMNH 2063 (6), trib. to Beach Cr., 2.9 airmi NNE Tallapoosa, Ga Hwy 120; UAIC 9037.09 (10), UAIC 9038.02 (3), UAIC 9039.02 (18), UAIC 9049.03 (9), UAIC 9050.02 (9), UAIC 9051.04 (17), and UAIC 1103.02 (1), Beach Cr., Ga Hwy 120, between Tallapoosa and Buchanan; UGAMNH 2065 (14), Holcomb Cr., trib. to Beach Cr., 0.1 mi S Ga Hwy 120, 4.1 airmi ENE Tallapoosa; UGAMNH 2068 (12), trib. to Tallapoosa R., 0.2 mi upstream of Co. Rd. 353/S2340 bridge, 4.6 airmi WSW Buchanan; UGAMNH 2053 (26) and UGAMNH 2070 (18), Flatwood Cr., 1.6 airmi NE Poplar Springs, Co. Rd. 194; UGAMNH 2066 (19), trib. to Tallapoosa R., 0.3 mi E Co. Rd. 191, 5.2 airmi WNW Buchanan; UGAMNH 2056 (7), Big Cr., trib. to Lassetter Cr., Co. Rd. 195, 2.8 airmi WNW Abernathys Mill; UGAMNH 2064 (6), Lassetter Cr., Co. Rd. 314, 6.8 airmi NNW Buchanan; UAIC 1104.06 (4), UGAMNH 2057 (2), and UGAMNH 2069 (4), Tallapoosa R., 4.2 mi N Buchanan, US Hwy 27; UAIC 1251.10 (6), Wircher Cr., 3.5 mi N Ga Hwy 120, 2.5 mi W junction Ga Hwy 120 and 101. PAULDING COUNTY: UAIC 1249.10 (4), Thomasson Cr., 2 mi SW Yorkville; UAIC 1248.12 (12), White Cr., trib. to Wircher Cr., 1.3 mi W Ga Hwy 101, 3 mi N junction Ga Hwy 120 and 101; UGAMNH 1548 (3), Tallapoosa R. at Co. Rd. 180; UAIC 1250.11 (1), McClendon Cr., 0.8 mi N Ga Hwy 120, 2.5 mi W junction Ga Hwy 120 and 101; UAIC 1247.07 (2), McClendon Cr. at Ga Hwy 101, 1.5 mi N junction Ga Hwy 120 and 101.

DIAGNOSIS: *Etheostoma tallapoosae* is a member of subgenus *Ulocentra* as diagnosed by Bouchard (1977) and Bailey and Etnier (1988). Further, *E. tallapoosae* lacks a premaxillary frenum and frequently has vomerine teeth, as is typical of members of the *E. duryi* species group of Bailey and Etnier (1988). In subgenus *Ulocentra*, coloration or combinations of color patterns in nuptial males are typically diagnostic. Nuptial males of *Etheostoma tallapoosae* are similar in general color pattern to males of several undescribed *Ulocentra* species of the Gulf Coastal Plain, but differ in having a row of (7–) 8–9 (–10) vertically oval to quadrate-shaped chocolate-brown blotches along the lateral line. These blotches are darkest and best defined anteriorly, and gradually fade to brownish orange or orange on the caudal peduncle (Figure 1). The blotches may be centered on the lateral line as in the color photograph, or mostly above the lateral line, especially in small or less intensely colored males. Some nuptial males have blue-green pigment present between the orange-covered, brown blotches. The uniformly broad central band of coloration in the spinous dorsal fin of the nuptial male is deep red posteriorly and gradually becomes dull brown anteriorly. *Etheostoma tallapoosae* lacks a red ocellus in the first membrane of the spinous dorsal fin, as do the undescribed *Ulocentra* species from the Gulf Coastal Plain, except for a species in the Black Warrior River system of the upper Mobile Basin.

DESCRIPTION: *Etheostoma tallapoosae* reaches a maximum of 56 mm SL (females) to 64 mm SL (males). Sexual dimorphism and apparent sexual maturity occur after 1 year's growth at about 30 mm SL (females) and 33 mm SL (males).

Frequency distributions of scale, fin ray, vertebral, and branchiostegal ray counts are presented in Tables 1-6. Lateral line complete with (44–) 47–53 (–57) scales. Transverse scale rows (13–) 14–17 (–18). Caudal peduncle scale rows (15–) 17–20 (–22). Dorsal fin with (9–) 10–11 (–12) spines and (10–) 11–12 (–13) soft rays. Anal fin with 2 spines and (6–) 7–8 (–9), modally 7, soft rays. Pectoral fin rays (13–) 14–15. Branchiostegal rays (5—4) 5—5 (6—6). Vertebrae 37–38 (–39). Cephalic sensory canals complete with 17 (1), 18 (48), or 19 (1) preoperculomandibular canal pores (sum of counts from left and right sides). Gill rakers 8 (8), 9 (15), or 10 (2), with length of longest rakers 2 to 3 times their basal width. Belly, opercle, cheek, nape, and prepectoral area covered with exposed scales. Some individuals have a mixture of exposed and embedded scales on the cheek. The breast is completely naked.

Proportional measurements appear in Tables 7-8. The males of *E. tallapoosae* have longer spinous and soft-rayed dorsal fins and longer anal fins, whereas females have greater body width, this presumably reflecting the gravid condition of some of the specimens.

Colors of living and freshly preserved nuptial individuals collected in March and April are described from Gold Branch specimens. Males with lower sides and ventral surface blotched dull brownish-orange anteriorly, becoming burnt orange posteriorly (Figure 1). The orange blotching extends dorsad to lower ends of 2 dark brown lateral blotches above anterior end of anal fin, and typically the burnt orange pigment is suffused over the last 2 or 3 lateral brown blotches (Figure 1). The anterior lateral brown blotches, as described in the

TABLE 1. Frequency distribution of lateral-line scale counts in three species of *Ulocentra* (count for holotype in boldface).

	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	N	$\bar{x}$	S.D.
Etheostoma tallapoosae			1	1	4	9	26	28	43	26	**25**	14	6	3	3	1		190	50.2	2.19
Etheostoma coosae			2	2	1	11	13	27	16	23	17	8	6	3	1	1	2	133	50.3	2.54
Etheostoma brevirostrum	1		3	8	16	11	21	21	18	11	7	3	**2**					122	48.5	2.32

TABLE 2. Frequency distribution of transverse scale rows (anal to spinous dorsal) in three species of *Ulocentra* (count for holotype in boldface).

	12	13	14	15	16	17	18	19	N	$\bar{x}$	S.D.
Etheostpma tallapoosae		3	36	**66**	67	16	2		190	15.3	0.97
Etheostoma coosae	2	14	48	34	24	9	1	1	133	14.7	1.23
Etheostoma brevirostrum	1	5	**64**	39	13	1			123	14.5	0.80

TABLE 3. Frequency distribution of number of scales around caudal peduncle in three species of *Ulocentra* (count for holotype in boldface).

	15	16	17	18	19	20	21	22	N	x̄	S.D.
Etheostoma tallapoosae	1	5	48	50	**52**	23	10	1	190	18.4	1.26
Etheostoma coosae	1	5	34	31	35	22	5		133	18.3	1.27
Etheostoma brevirostrum		1	44	**37**	36	4			122	18.0	0.91

TABLE 4. Frequency distribution of dorsal fin ray counts in three species of *Ulocentra* (count for holotype in boldface).

	Dorsal spines							Dorsal soft rays						
	9	10	11	12	N	x̄	S.D.	10	11	12	13	N	x̄	S.D.
Etheostoma tallapoosae	3	**90**	85	12	190	10.5	0.64	4	99	**83**	4	190	11.5	0.56
Etheostoma coosae	18	81	33	1	133	10.1	0.63	10	63	55	5	133	11.4	0.69
Etheostoma brevirostrum	5	41	**71**	6	123	10.6	0.64	26	**78**	19	123	10.9	0.60	

TABLE 5. Frequency distribution of fin ray counts in three species of *Ulocentra* (count for holotype in boldface).

	Anal soft rays								Left pectoral rays								
	5	6	7	8	9	N	$\bar{x}$	S.D.	11	12	13	14	15	16	N	$\bar{x}$	S.D.
Etheostoma tallapoosae		7	**126**	56	1	190	7.3	0.53			17	**140**	33		190	14.1	0.51
Etheostoma coosae		6	75	50	2	133	7.4	0.59			40	86	7		133	13.7	0.54
Etheostoma brevirostrum	1	5	87	**30**		123	7.2	0.53	1	1	42	**79**			123	13.6	0.55

TABLE 6. Frequency distribution of number of vertebrae and number of branchiostegal rays in three species of *Ulocentra* (count for holotype in boldface).

	Vertebrae							Branchiostegal Rays							
	37	38	39	40	N	$\bar{x}$	S.D.	5—4	5—5	6—5	5—6	6—6	7—6	7—7	N
Etheostoma tallapoosae	25	**91**	7		123	37.8	0.49	1	**180**	4	4	1			190
Etheostoma coosae	4	47	26		77	38.3	0.56		4	4	3	119	2	1	123
Etheostoma brevirostrum	9	30			39	37.8	0.43		**117**	3	1	2			123

diagnosis, are distinct because the surrounding surface is more or less of a uniform shade of pale brown. The middorsal area from occiput to the upper caudal fin base is typically blotched with 8 dark brown saddles. Some nuptial males taken from the lower Gold Branch site on 12 April 1990 displayed aquamarine to green coloration between the last 3 lateral brown blotches and this color also was suffused over the 2 saddle blotches on the caudal peduncle. The upper surface of head is dark brown, a few dark brown spots are present on upper part of opercle and cheek, and the slightly curved suborbital bar, preorbital bar, and iris are black. The lower lip, gular area, branchiostegal membranes, isthmus, lower part of cheek and opercle, and breast are bright blue-green. The pelvic and anal fins of the nuptial male are generally heavily pigmented with melanophores but exhibit considerable blue-green coloration, particularly the anal fin. The pelvic fin has some golden color suffused over anterior part of fin, and tips of the rays are milky white. The spinous and anterior soft rays of anal fin and their distal tips are milky white. The dark blue-green on the membranous areas contrasts with the milky white color on rays (Figure 1). The upper and lower margins (procurrent rays) of caudal fin are bright blue-green. The most prominent coloration of the caudal fin is the 2 elongate burnt orange blotches, 1 above and 1 below the typically paired basicaudal dark spots. The burnt orange blotches are continuous or nearly so with the burnt orange color that is suffused over the posterior lateral blotch. The rest of the caudal fin is a mixture of yellow, olive, and blue-green color. The spinous dorsal fin has a narrow pale blue border. Proximal to this is a thin line of milky white pigment and between the milky white line and a basal band or row of black blotches is a relatively broad central band. This central band is deep red posteriorly, becoming brownish anteriorly. The red covers much of the membranous area at the posterior part of fin but narrows to the central part of each membrane anteriad. Above and below the central red area the membranes are brownish with golden flecks. Below (proximal to) the band of black blotches there is a shortened narrow band of golden brown (emphasized on rays). At the central base of the spinous dorsal fin the dark brown of the dorsal saddle patch extends onto the base of the central 4 dorsal spines and associated membranes (Figure 1). The soft dorsal fin has a prominent median red band extending from posterior rays (where it is best developed and occupies over half the height of the fin) to the anterior ray (Figure 1). Anteriorly the red band occupies about one-third the fin height and becomes more separated into individual blotches on each interradial membrane. The distal margins of the separated projections are edged with yellow pigment. The fin distal and proximal to the red band is bluish gray. There is some extension of dark brown pigment onto the bases of the fin rays at the dorsal saddle blotch at the anterior end of the soft dorsal fin. The interradial membranes of the pectoral fin are essentially clear. The rays are moderately pigmented with melanophores and a superficial covering of yellow and golden pigment. Nuptial females have lower side and ventral surface of head and body immaculate white. The dark preorbital bar, dark suborbital bar, and several dark spots on upper part of cheek and opercle stand out against the immaculate white of the lower surface of the head.

TABLE 7. Measurements in thousandths of standard length for *Etheostoma tallapoosae*, *E. coosae* and *E. brevirostrum*, males.

	E. tallapoosae (N = 25)			*E. coosae* (N = 25)			*E. brevirostrum* (N = 25)		
	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.
Standard length (mm)	43.2–61.2	48.8	3.8	40.5–57.4	50.1	4.3	38.6–49.0	45.3	2.6
Head length	236–262	249	8.1	244–269	254	7.1	235–255	244	4.5
Body depth at dorsal origin	191–220	203	8.6	190–221	207	9.2	186–206	197	5.9
Snout length	66–79	72	4.0	62–74	69	3.3	62–75	70	3.2
Orbit length	57–67	63	2.6	59–71	66	2.6	59–75	65	3.2
Spinous dorsal fin length	265–308	290	10.6	271–304	287	12.0	265–315	290	13.1
Longest dorsal spine	99–142	120	10.9	107–143	130	8.4	114–154	132	8.8
Soft dorsal fin length	242–276	260	9.3	275–343	314	20.1	238–280	260	10.4
Longest dorsal soft ray	114–146	134	7.7	148–204	176	15.5	136–156	145	5.0
Caudal peduncle length	293–328	310	9.0	288–315	303	7.4	260–307	288	13.1
Caudal peduncle depth	99–113	106	3.7	98–114	106	4.6	102–116	107	2.4
Anal fin length	227–276	246	11.4	244–288	269	14.6	230–268	247	9.3
First anal spine length	61–76	66	3.7	53–84	72	8.4	71–98	82	6.4
Longest anal soft ray	111–144	129	7.8	121–179	146	13.1	124–157	137	8.3
Caudal fin length	176–216	202	10.9	193–241	221	12.5	188–228	211	9.3
Pectoral fin length	221–271	250	14.3	227–301	269	18.7	255–295	279	9.8
Pelvic fin length	194–245	220	10.6	191–247	216	14.5	209–245	227	9.5
Trans-pelvic width	74–87	82	2.7	72–86	79	3.1	77–88	84	2.6
Maximum body width	126–164	142	7.4	119–142	131	6.5	122–157	146	6.8
Interorbital width	41–48	44	1.9	37–47	44	2.3	42–52	45	1.9

TABLE 8. Measurements in thousandths of standard length for *Etheostoma tallapoosae*, *E. coosae* and *E. brevirostrum*, females.

	E. tallapoosae (N = 10)			*E. coosae* (N = 10)			*E. brevirostrum* (N = 10)		
	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.
Standard length (mm)	38.2–45.5	42.6	2.3	42.7–50.2	45.0	2.1	42.9–47.1	44.3	1.5
Head length	238–257	245	6.1	238–263	250	8.1	230–254	242	8.1
Body depth at dorsal origin	198–219	211	9.1	202–227	216	7.4	181–196	189	4.8
Snout length	68–73	70	1.9	60–68	65	2.9	64–71	67	2.9
Orbit length	63–68	65	1.5	66–72	69	2.1	63–66	65	0.9
Spinous dorsal fin length	263–290	275	8.9	244–285	262	10.8	264–290	277	8.3
Longest dorsal spine	96–114	108	5.9	95–119	106	6.8	105–118	110	5.6
Soft dorsal fin length	240–262	251	6.9	251–288	266	12.1	236–264	253	10.7
Longest dorsal soft ray	126–156	138	8.9	131–159	144	8.5	130–148	142	6.1
Caudal peduncle length	299–316	305	9.2	295–306	302	3.7	272–296	282	7.3
Caudal peduncle depth	97–104	101	1.9	94–108	100	3.9	95–109	101	4.4
Anal fin length	220–261	237	13.6	220–244	231	9.1	222–246	230	6.8
First anal spine length	61–70	65	2.8	47–69	58	7.1	68–84	74	5.6
Longest anal soft ray	113–142	126	9.2	115–144	130	9.1	126–140	135	5.2
Caudal fin length	194–222	204	8.0	207–239	221	10.3	190–212	202	6.4
Pectoral fin length	236–273	255	11.3	254–295	273	12.9	256–302	276	16.5
Pelvic fin length	201–233	215	9.7	185–229	210	12.3	201–228	218	7.4
Trans-pelvic width	80–87	83	2.3	71–81	77	2.7	77–84	81	2.4
Maximum body width	139–170	153	13.1	137–166	150	9.0	141–158	147	5.2
Interorbital width	42–47	44	1.6	42–47	45	1.5	41–47	44	2.4

Most large females have some xanthic coloration. Often the female will have the 2 elongate (reduced in size) orange blotches on base of caudal fin, at least a posterior segment of red band in soft dorsal fin, and some orange on the lower sides. A few females had some red pigmentation on posterior central part of spinous dorsal fin. The rest of the dorsal part of the females is pigmented with various shades of brown. Invariably there is a dark brown blotch on the prepectoral area of females of all sizes. The 8–10 dark brown lateral blotches extend from the lateral line or a little above it ventrad to well below the lateral line, so that the lower two-thirds are well contrasted against the immaculate white of the lower side and belly. The lateral blotches of the females are not as uniformly nor as densely pigmented as those of the nuptial males. The upper side and dorsum is a continuous patchwork of various shades of brown, usually with 8 dorsal saddle marks. The upper area of the head is a uniform dark brown. The pelvic and anal fins are immaculate. The lower part of the pectoral fin is immaculate whereas there are dark blotches on the rays of the upper two-thirds of the fin and when the fin is spread the blotches tend to form wavy bars. The caudal fin has a similar pattern as that described for pectoral fin. There are typically 2 well separated dark elongate blotches at the base of the caudal fin. Both the spinous and soft dorsal fins also have dark blotches spaced along the rays, and a varying amount of pigment on the membranous areas.

The blues, greens, and blue-greens fade rapidly after preservation whereas the reds, oranges, and yellow fade more gradually, and some of this xanthic color may persist for several months.

DISTRIBUTION: *Etheostoma tallapoosae* is confined to the Tallapoosa River system above the Fall Line in the Blue Ridge and Piedmont physiographic provinces (Figure 4). Although the species is widespread throughout the system in Alabama and Georgia, there has been considerable habitat loss in recent years because of impoundment and small stream deterioration. *Etheostoma tallapoosae* is primarily an inhabitant of small to medium-size streams but does occur in the main channel of the upper Tallapoosa and Little Tallapoosa rivers.

HABITAT AND BIOLOGY: Gold Branch at Ala Hwy 63 (type locality) was a small stream 2 to 15 feet wide with a substrate of boulders, rubble, gravel, sand, and a few silted areas during the 1950s. Sometime between the 1960s and the mid-1980s, Ala Hwy 63 was straightened, widened, and somewhat elevated over Gold Branch. The deposition of large chunks of limestone rip-rap upstream and downstream of the new concrete culvert drastically modified the stream habitat. The land along Gold Branch above the culvert was cleared and is now a heavily grazed pasture. Spring floods have produced a deep plunge pool below the highway culvert. Thus most of the area where the early collections were made is now unsuitable darter habitat. All recently collected specimens were taken downstream from the cleared highway right-of-way, where the substrate consists of boulders and rubble, with some gravel and stretches of sand.

Based on our observations and examination of specimens in other museums, spawning takes place during March and April. There is some evidence that breeding colors of males begin to intensify in February and perhaps as early as late January. Samples taken during mid-May exhibited post-reproductive condi-

tions. Females outnumber males in the breeding concentrations. An analysis of three samples, two from the type locality, 16 March 1957 (type series), and 12 April 1966, and one from Enitachopco Creek, 13 April 1966, revealed 52 males vs 85 females, 18 males vs 27 females, and 19 males vs 38 females, respectively. Summation of the three collections results in 89 (37%) males vs 150 (63%) females. All individuals in these samples were considered to be adults based on nuptial coloration of males and elongate genital papilla of females. Males ranged in size from 33–61 mm SL ($\bar{x}$ = 44.8 mm, SD = 4.7124) and females ranged in size from 30–52 mm SL ($\bar{x}$ = 38.4 mm, SD = 4.3350).

The species associates of *Etheostoma tallapoosae* at the type locality, based on six collections taken between 5 October 1955 and 12 April 1990, are as follows: *Hypentelium etowanum*, *Campostoma anomalum*, *Hybopsis lineapunctata*, *Nocomis leptocephalus*, *Notropis baileyi*, *N. chrysocephalus*, *N. gibbsi*, *N. texanus*, *N. venustus*, *Semotilus atromaculatus*, *Fundulus bifax*, *Lepomis auritus*, *L. macrochirus*, *Micropterus coosae*, and *Cottus carolinae*. A few miles downstream at the Elmore County 357 road crossing of Gold Branch several additional species were taken in three samples: *Moxostoma poecilurum*, *Notropis bellus*, and *Percina* (*Alvordius*) sp.

ETYMOLOGY: The epithet *tallapoosae* refers to the Tallapoosa River.

Etheostoma brevirostrum, new species
Holiday Darter
Figures 2 and 4

Etheostoma (*Ulocentra*) sp. Boschung, 1961: 280 (misidentification of *E. coosae*). Smith-Vaniz, 1968: 102 (characterization and distribution). Stiles and Etnier, 1971: 15 (Conasauga River, Tennessee, records). Jenkins, 1976: 646 (distribution).

Etheostoma sp. Ramsey, 1976: 63-64 (distribution, habitat description, Alabama records). Kuehne and Barbour, 1983: 98-99, *pl. 12* ("upland snubnose darter," characterized, range map). Sizemore and Howell, 1990: 3-5 ("upland snubnose darter," distribution in springs).

HOLOTYPE: Adult male, TU 158216, 40.7 mm standard length, Shoal Creek, tributary to Choccolocco Creek at Pine Glen Recreation Area, 8.1 mi N of US Hwy 78, (T15S, R10E, Sec 16), Cleburne County, Alabama, 10 May 1989, R. D. Suttkus and J. Malcolm Pierson.

PARATOPOTYPES: TU 154765 (6, 34-42), collected with holotype; AUM 1588 (5, 34-47), 13 August 1968; TU 56167 (2, 27-32), 26 January 1969; TU 60351 (5, 35-42), 16 October 1969; AUM 9349 (1, 42), 6 August 1974; AUM 13639 (3, 28-45), 30 September 1976; UAIC 6420.04 (2, 39-41), 6 April 1981; UAIC 6626.07 (2, 39-42), 11 April 1982; UAIC 7162.01 (2, 34-40), 23 July 1984; TU 152214 (2, 32-37), 13 May 1988.

OTHER PARATYPES: COOSA RIVER SYSTEM, ALABAMA. CALHOUN COUNTY: TU 60687 (2, 37-44), Shoal Cr., 2.3 mi E White Plains at Whitesides Mill, T15S, R9E, Sec 12, October 1966; TU 57896 (1, 35), 17 June 1969; TU 66257 (5, 33-46), 15 December 1970; TU 68585 (3, 34-36), 17 March 1971; TU 74352 (1, 36), 7 December 1971; and AUM 6086 (1, 43), 4 October 1972, all from same locality; TU 59644 (64, 29-48), same locality, 14 October 1969, distributed as follows: TU 59644 (44), ANSP 167317 (2), AUM 25936 (2), CU 72360 (2),

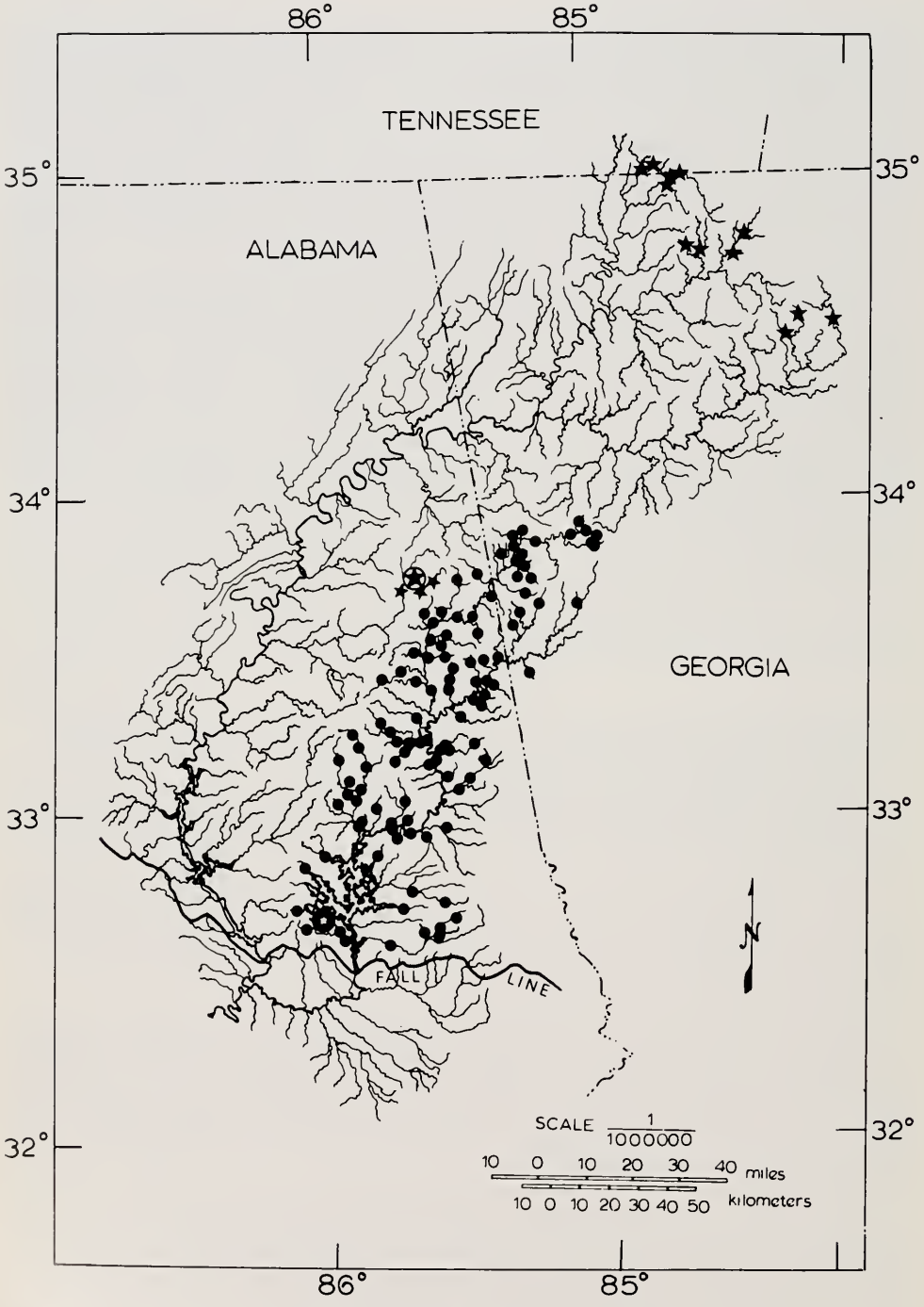


Figure 4. Distribution of *Etheostoma tallapoosae* (solid dots, type locality open star in solid spot), and *Etheostoma brevirostrum* (solid stars, type locality solid star in open circle).

INHS 59306 (2), SIUC 18164 (2), UAIC 10017.01 (2), UGAMNH 2168 (2), UMMZ 218252 (2), USNM 314353 (2), and UT 91.3926 (2); TU 66556 (1, 34), Choccolocco Cr., 1.0 mi S White Plains, Ala Hwy 9, T15S, R9E, Sec 10, 15 December 1970; AUM 11492 (3, 40-46), Shoal Cr., 5.6 airmi NW Heflin, 0.2 mi W Cleburne Co. line, T15S, R9E, Sec 24, 6 August 1974; UAIC 6489.01 (1, 48), Little Shoal Cr. at Forest Service Rd. 531, Talladega National Forest, 16 November 1980.

ADDITIONAL MATERIAL EXAMINED BUT NOT DESIGNATED AS TYPES: COOSA RIVER SYSTEM, GEORGIA. GILMER COUNTY: CU 28298 (9), Rock Cr., 7.8 mi SW Blue Ridge, 8.4 mi NE Ellijay, US Hwy 76, 3 September 1953; TU 12270 (11), same locality, 9 October 1955; FSU 2442 (8), Bear Cr., 10.3 mi NW Ellijay, 9 October 1955; TU 32784 (12), same locality, 2 June 1964; TU 38262 (1), same locality, 20 June 1965; UT 91.2105 (1), Big Turniptown Cr., 3 mi NE Ellijay, Ga Hwy 5, 13 April 1980; UT 91.2104 (2), Mountaintown Cr., 5 airmi NW Ellijay, 12 April 1980; TU 27979 (3), Conasauga Cr., trib. to Mountaintown Cr., 9.3 mi W Ellijay, US Hwy 76, 31 May 1962. MURRAY COUNTY: UT 91.1230 (1), Conasauga R., 1 mi upstream of confluence with Jacks R., 4 August 1966; UAIC 9029.05 (2), Jacks R. at Tennessee/Georgia line, 22 August 1981; UT 91.1688 (8), Conasauga R., 1.8 airmi S Tennessee/Georgia line, 0.8 mi SW Hopewell Church, Ga Hwy 2, 1 October 1978; UGAMNH 2062 (1), Conasauga R., 6.3 airmi NE Cisco along Ga Hwy 2, upstream of Hwy 2 crossing, August 1983. DAWSON COUNTY: UAIC 2910.04 (1), Amicalola Cr., 3.7 mi SW Johntown, 9.5 mi N Dawsonville, 18 April 1968; UGAMNH 2059 (1), Amicalola Cr., Co. Rd. 25, 1.8 airmi SSW junction Ga Hwy 136/183, 8 May 1990; UGAMNH 2060 (4), Cochran Cr., Co. Rd. 45, 1.0 airmi SW of junction Ga Hwy 52/342, 8 May 1990. LUMPKIN COUNTY: UGAMNH 2052 (1), Etowah R., Ga Hwy 52, 13 May 1990; UAIC 9811.09 (1), same locality, 1 June 1990.

COOSA RIVER SYSTEM, TENNESSEE. POLK COUNTY: UT 91.343 (1), Conasauga R., Boanerges Church bridge, 14 October 1969; UT 91.348 (2), Conasauga R., ford above US Hwy 411, 11 October 1969.

DIAGNOSIS: *Etheostoma brevirostrum* is a member of the subgenus *Ulocentra* as diagnosed by Bouchard (1977) and Bailey and Etnier (1988). Further, *E. brevirostrum* often has vomerine teeth and either lacks the premaxillary frenum or has a poorly developed one. Being similar to *E. etnieri* in this respect, we place *E. brevirostrum* in the *E. duryi* species group (Bailey and Etnier, 1988). It differs from all members of subgenus *Ulocentra* except *E. etnieri* and *E. pyrrhogaster* in having a median red band in the anal fin of nuptial males, and from both of those species in having a narrow (vs broad) red band in the soft dorsal fin, in addition to many other aspects of male coloration. Colors of breeding males of this species are perhaps the most distinctive of any species in the subgenus. The red blotches on the lower side are haloed by white and bright yellow. The yellow tends to fade rapidly and very little remains after a few minutes in preservative. *Etheostoma brevirostrum* has a red ocellus in the first membrane of the spinous dorsal fin (Figure 2), as do *E. coosae* and the undescribed *Ulocentra* species from the Black Warrior River system; this ocellus is lacking in *E. tallapoosae* and the several undescribed *Ulocentra* species from the area south of the Tennessee River. The red color often present on the basal part of the pelvic fins of nuptial males is absent from other species of *Ulocentra*.

DESCRIPTION: *Etheostoma brevirostrum* reaches a maximum of 47 mm SL (females) to 53 mm SL (males). Frequency distributions of scale, fin ray, vertebral, and branchiostegal ray counts are presented in Tables 1-6. Lateral line complete with (42–) 45–52 (–54) scales. Transverse scale rows (12–) 14–16 (–17). Caudal peduncle scale rows (16–) 17–19 (–20). Dorsal fin with (9–) 10–11 (–12) spines and 10–12 soft rays. Anal fin with 2 spines and (5–) 7–8, modally 7, soft rays. Pectoral fin rays (11–) 13–14. Vertebrae modally 38. Branchiostegal rays

5—5 (6—6). Cephalic sensory canals complete with 16 (1), 17 (6), 18 (42), or 19 (1) preoperculomandibular canal pores (sum of counts from left and right sides). Gill rakers 8 (6), 9 (15), or 10 (4), with length of longest rakers 2 to 3 times their basal width. Belly, opercle, cheek, and nape typically covered with exposed scales. Some individuals have a mixture of exposed and embedded scales on the cheek. Scalation variable on prepectoral area; some specimens have only a few scales whereas others have entire area covered with scales. The breast is completely naked. Proportional measurements are presented in Tables 7-8. The males of *E. brevirostrum* have median and pelvic fin lengths greater than those of females.

Colors of freshly preserved nuptial specimens are described from Shoal Creek specimens collected 13 May 1988 and 10 May 1989. Males with a prominent row of red blotches (several triangular in shape) along lower side, each blotch, and the 2 elongate red blotches at base of caudal fin, distinctly haloed with yellowish-cream to white. There is another row of small haloed red blotches along upper side of caudal peduncle and forward on upper side to below anterior insertion of spinous dorsal fin. Between the haloed blotches along lower side the surface is bright green or blue-green and this color forms 5 or 6 vertical bars from just anterior to the anal fin to the caudal fin base. Upper and lower caudal rays, including procurrent rays, are bright green or blue-green, whereas the rest of the caudal fin is less intense green and there is considerable yellowish or golden pigment along the central rays. Along the lateral line the green pigmented areas are darkened with black or dark brown, particularly on anterior half of body. There is a row of brown blotches anteriorly just above the lateral line. The brown blotches diminish in size posteriorly and become blended with the haloed red blotches. The entire dorsum is green and the dorsal saddle marks are darkened with melanophores. The occiput, snout, and breast are bright green. The cheek, opercle and gill membranes were a faint blue-green at time of capture (10 May 1989) but faded quickly.

The anal fin is distinct in coloration, having a wide, bright red diagonal band across the middle of the fin that is otherwise a solid blue-green color with a bit of milky white on the tips of the rays. The pelvic fins have a small blotch of bright red at base of median rays, whereas most of the rest of the fin is a solid blue-green color with a milky white anterior and distal border. The membranes of the pectoral fin are clear, but the rays have a light sprinkling of xanthic coloration. The second dorsal fin has a prominent, narrow red band that extends from the posterior edge of fin anterior to the second or third interradial membrane. The upper and lower margin of red band is edged with yellowish-cream. The rest of the fin distal, anterior, and proximal to the red band has a light wash of blue-green, and there is an inconspicuous, interrupted black band above and below (but not contacting) the red band, with this pigment mostly on the membranes. There is a speckling of red on 1 or 2 rays anterior to red band. The spinous dorsal fin has a broad, centrally located red band. The band is broad and intense red on the last 3 or 4 interradial membranes, and gradually diminishes in intensity and width anteriad to the second interradial membrane. On the first interradial membrane the red is intense and forms the typical red ocellus that is present in many members of the subgenus. Both distally and

proximally the red band is bordered by yellowish-cream or milky white. The outer edge of the fin is blue-green, with this band wider and more intense blue-green posteriad. The area proximal to the red band also is blue-green but a basal row of dusky spots tends to mask the color.

Females are much less colorful than males. Green is moderately developed on lateral blotches, on blotches on upper side, and on dorsal saddles. The anterior end of anal fin, upper and lower procurrent areas of caudal fin, breast, gill membranes, and gular area are pale blue-green. The nuptial female has greatly reduced red blotches on lower side and these are haloed with yellowish white. The elongate blotches at base of caudal fin are smaller and orange-red in contrast to the large, bright red blotches of the nuptial male. There are red blotches of reduced size on the upper side from base of caudal fin anteriad. The anterior blotches in this series are greatly suffused with brown. The caudal and second dorsal fins (and to a lesser extent the first dorsal fin) have dark blotches on the rays that are aligned to form dark bands, and the rays are otherwise bright yellow to cream colored. All five nuptial females taken from Shoal Creek on 10 May 1989 had a bright red ocellus on the first interradial of the spinous dorsal fin. Additional dorsal fin red pigment is reduced to a small spot posteriad in the second dorsal and small red spots in the posterior six or so membranes of the spinous dorsal.

In preservative, nuptial males have the breast, venter, and lower side densely pigmented with small melanophores. A few of the central areas formerly covered by the bright red blotches are lightly pigmented. The anal fin is heavily pigmented except where the red band was present and this area is now pale. The 2 basicaudal areas (formerly red) are only lightly pigmented. The basicaudal dark pigment may form a single, median spot, a short vertical bar with an upper and lower posterior projection, or 2 distinct parallel blotches separated by a pale area. The pelvic fins are heavily pigmented except for pale distal tips and anterior margin of first spine. Pectoral and caudal fin membranes are clear, and the interrupted patches of pigment on the rays form wavy bands. Most of the membranous areas of both the spinous and the soft dorsal fins are heavily pigmented with small melanophores. The areas formerly covered with red pigment, not yet entirely faded, are less densely pigmented with melanophores. The faded ocellus now appears as a pale window. Although the opercle, cheek, lateral snout area, and prepectoral area are rather heavily pigmented, the preorbital bar, suborbital bar, 2 or 3 spots on upper cheek and opercle, and 1 or 2 spots on prepectoral area are darker and contrast rather markedly with the paler background.

Nuptial females in preservative show very little dark pigment on the lips, gular area, isthmus, gill membranes, lower cheek, lower opercle, breast, belly, or areas formerly covered with red on the lower side and caudal peduncle. Some females have a small patch of melanophores located on mid-ventral part of gill membrane and a few individuals have a few melanophores on anterior border of breast and on genital papilla. There is some pigment on all fins; the pelvic and anal fins have the least. The pectoral, caudal, and both portions of the dorsal fin have interrupted patches of pigment on the rays, and when the fins are spread, wavy bands are formed. The membranous areas of the pectoral,

pelvic, anal, and caudal fins of the females are immaculate. There is a varying amount of dark pigment on membranes of the spinous and soft-rayed dorsal fins. The melanophores are mostly on the posterior membranous areas on the soft dorsal but may be on both the posterior and anterior membranes of the spinous dorsal fin. The dark preorbital bar, suborbital bar, spots on upper cheek and opercle, prepectoral spot, and lateral blotches (formerly suffused with green) contrast with the immaculate ventral area. The dark lateral blotches on the caudal peduncle extend all the way to the midventral part of the caudal peduncle in some females. Basicaudal dark pigment is as described for males.

DISTRIBUTION: *Etheostoma brevirostrum* is confined to the Coosa River system above the Fall Line, in the Valley and Ridge and Blue Ridge physiographic provinces. Our records show that *E. brevirostrum* has a disjunct distribution. The small isolated population in the middle and lower stretches of Shoal Creek, a tributary to Choccolocco Creek, is the only locality in Alabama. There are scattered locality records in the upper Conasauga River in northern Georgia and southern Tennessee, a few localities in the upper Coosawattee River system in northern Georgia, and a few localities in the upper Etowah River system in north-northeast Georgia (Figure 4). Two reservoirs, Whitesides Mill Lake and Highrock Lake, have possibly eliminated *Etheostoma brevirostrum* from the Calhoun County, Alabama, section of Shoal Creek. To our knowledge, no specimens have been taken from the area subsequent to the impoundments. Sizemore and Howell (1990) reported 13 specimens from three large springs in the Choccolocco Creek system.

HABITAT AND BIOLOGY: We have designated Shoal Creek at Pine Glen Recreation Area in Cleburne County, Alabama, as the type locality. Shoal Creek is 30 to 60 feet wide with a substrate of boulders, rubble, gravel, sand, and a few small silted areas. The water is usually clear with moderate to fast current. During the summer, beds of *Justicia* develop in the riffles and along the shallows. The banks are heavily wooded. During the 26 January 1969, 13 May 1988, and 10 May 1989 collections, Shoal Creek was clear, but during the 16 October 1969 collection it was high and very muddy. During January the water temperature was 5°C, May of 1988 it was 18°C, May of 1989 it was 17°C, and October of 1969 it was 16°C. In the upper Coosa system of Georgia and Tennessee, many *Etheostoma brevirostrum* localities are smaller and cooler than the type locality, and rooted macrophytes are absent. We know very little about the reproductive biology of *E. brevirostrum*. Based on our meager observations we assume that spawning takes place during April and May. The one nuptial male collected in 1988 and the two nuptial males collected in 1989 from Shoal Creek were taken from near boulders with small patches of sand between the boulders. The water was fast flowing, about 2–3 feet deep, 6–8 feet from the bank. Examination of UGAMNH 2060 (4), collected from Cochran Cr., Dawson Co., Georgia, on 8 May 1990 by B. J. and M. C. Freeman, and their color slide taken a short time after capture, indicate these specimens were in nuptial condition.

We have examined 185 specimens for this study and it is interesting that only 26 (14%) specimens (in 11 lots) were obtained in March, April, and May, the months during which *Ulocentra* species are aggregated for breeding and, in

our experience, most vulnerable to capture. The largest series were taken in September through December. The species associates of *Etheostoma brevirostrum* at the type locality, taken in four collections, are as follows: *Hypentelium etowanum*, *Moxostoma duquesnei*, *Campostoma anomalum*, *Notemigonus crysoleucas*, *Notropis asperifrons*, *N. callistius*, *N. trichroistius*, *N. xaenocephalus*, *Rhinichthys atratulus*, *Semotilus atromaculatus*, *Ictalurus natalis*, *Noturus leptacanthus*, *Ambloplites ariommus*, *Lepomis macrochirus*, *L. megalotis*, *L. microlophus*, *Micropterus coosae*, *Etheostoma coosae*, *E. jordani*, *Percina nigrofasciata*, *P. palmaris*, and *Cottus carolinae*.

Prior to the impoundment of Shoal Creek, the Whitesides Mill location was one our favorite collecting sites for *E. brevirostrum*. Based on two collections, one on 17 June 1969 and the other on 14 October 1969, we had the following cumulative species list: *Hypentelium etowanum*, *Moxostoma duquesnei*, *Campostoma anomalum*, *Notropis asperifrons*, *N. caeruleus*, *N. callistius*, *N. chrosomus*, *N. chrysocephalus*, *N. lirus*, *N. stilbius*, *N. trichroistius*, *N. venustus*, *N. volucellus*, *N. xaenocephalus*, *Phenacobius catostomus*, *Fundulus stellifer*, *Ambloplites ariommus*, *Lepomis gulosus*, *L. megalotis*, *Micropterus coosae*, *Etheostoma coosae*, *E. jordani*, *E. stigmaeum*, *Percina nigrofasciata*, *P. palmaris*, and *Cottus carolinae*. We hasten to add that the largest series (64 specimens) of *E. brevirostrum* was taken during the 14 October 1969 collection whereas only a single specimen was taken earlier that year, on 17 June.

ETYMOLOGY: The name *brevirostrum* is from the Latin *brevi* = short, and *rostrum* = beak or snout, and is descriptive of the short snout. This name was coined by John S. Ramsey in the early 1970s when he was actively studying the snubnose darters.

COMPARISONS: There is considerable overlap in meristic features among the three Alabama River system species compared here, *Etheostoma tallapoosae*, *E. coosae*, and *E. brevirostrum*, as shown in Tables 1-6. Although the modal vertebral count is 38 for all three, *E. coosae* averages higher than *E. tallapoosae* and *E. brevirostrum*. Both *E. tallapoosae* and *E. brevirostrum* typically have 5—5 branchiostegal rays, whereas *E. coosae* typically has 6—6 branchiostegals. Both *E. coosae* and *E. brevirostrum* have a red ocellus on the first interradial membrane of the spinous dorsal fin. *Etheostoma tallapoosae* lacks the ocellus, as do the several undescribed species of *Ulocentra* known from below the Fall Line, and these species have color patterns suggesting that they, rather than *E. brevirostrum* and *E. coosae*, represent the closest relatives of *E. tallapoosae*. An examination of Figures 1-3 discloses a number of differences in color patterns of the nuptial males. *Etheostoma brevirostrum* is the only one of the three having a red band across the anal fin. Both *E. tallapoosae* and *E. brevirostrum* have a moderately wide band of bright red across the middle of the second dorsal fin, whereas *E. coosae* has nearly the entire fin covered with a very broad band of dull red. *Etheostoma brevirostrum* is the only species having yellow-cream and white haloed red blotches on the lower side. There are additional differences in the details of the spinous dorsal pigmentation and the arrangement, shape, and color of lateral blotches. Tables 7 and 8 give a comparison of proportional measurements of the three species (expressed in thousandths of standard length). In spite of their visibly different profiles, standard snout length measurement is little different among the three

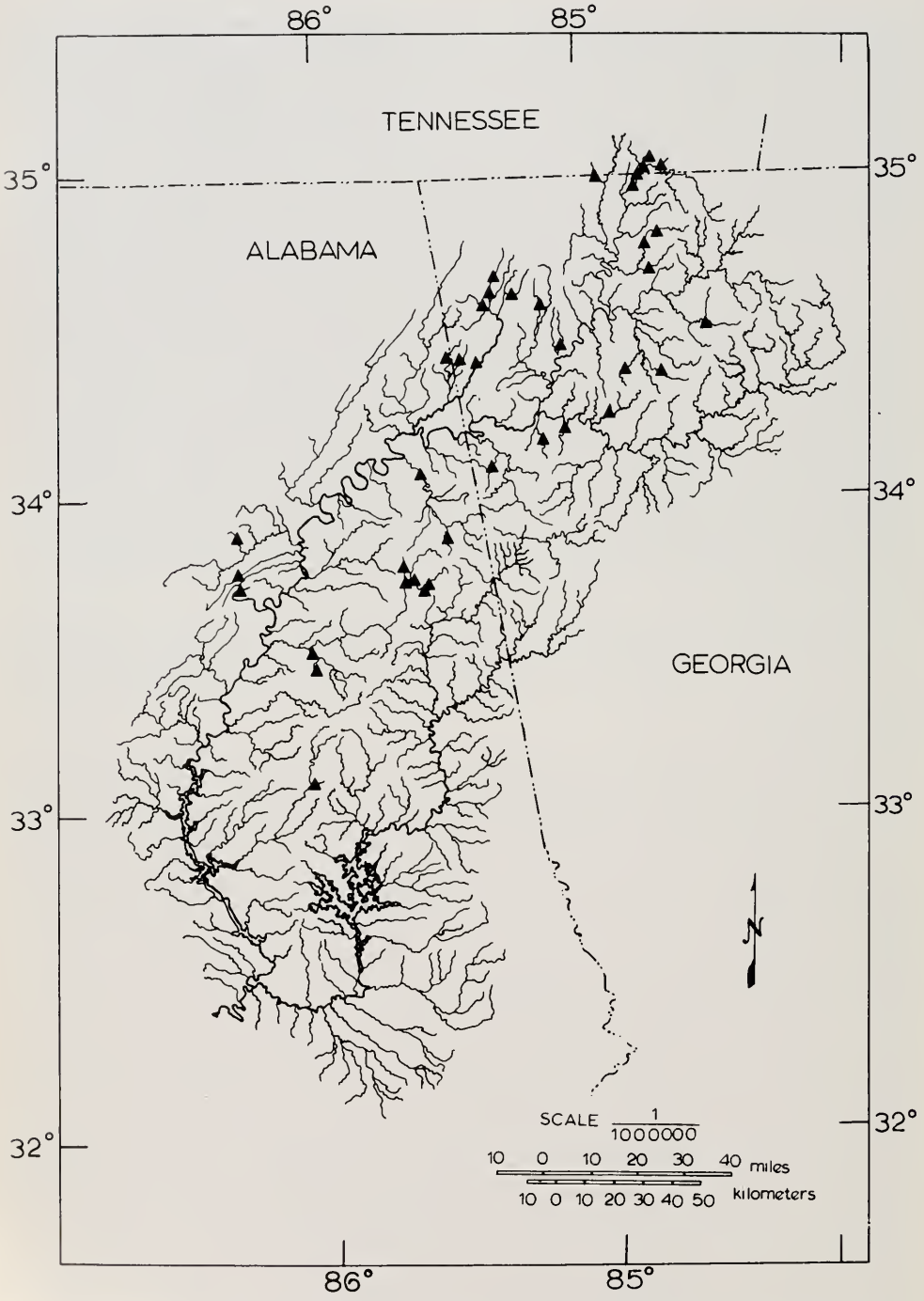


Figure 5. Distribution of *Etheostoma coosae* based on samples used for comparative material in his study.

species. The soft dorsal fin is longer in males and females of *E. coosae* than in either *E. brevirostrum* or *E. tallapoosae*. Both *E. tallapoosae* and *E. brevirostrum* males are similar in anal fin length, whereas male *E. coosae* have a longer anal fin. There is no apparent difference in anal fin length in females of the three species. *Etheostoma brevirostrum* has the longest first anal spine of the three species, with the difference apparent in both males and females.

Fowler (1945) described *Etheostoma coosae* using specimens collected from a small creek near Chesterfield, Cherokee County, Alabama. We collected additional topotypic material for our comparisons of *E. coosae* with *E. tallapoosae* and *E. brevirostrum*; the following is a list of collections of *E. coosae* that we used for the comparisons. The collection site records are presented on the drainage map of the Coosa River system (Figure 5).

COOSA RIVER SYSTEM, ALABAMA. Coosa County: TU 41138 (36), trib. to Hatchet Cr., 3.7 mi NE Goodwater, Ala Hwy 9. Talladega County: TU 71903 (16), Kelly Cr., trib. to Cheaha Cr., 5 mi SW Munford, Ala Hwy 21; TU 152199 (29), Cheaha Cr., T17S, R6E, Sec 33. Calhoun County: TU 69507 (1), Choccolocco Cr., 1 mi S White Plains, Ala Hwy 9; TU 59645 (4), Shoal Cr., 2.1 mi E White Plains; TU 40783 (23), Cottaquila Cr., trib. to Choccolocco Cr., 2.7 mi N White Plains, Ala Hwy 9. Cleburne County: TU 60352 (1), TU 152215 (27), and TU 154766 (10), Shoal Cr. at Pine Glen Recreation Area; TU 154789 (5), Terrapin Cr., Co. Rd. 55; TU 154750 (21), trib. to Shoal Cr., 7.1 mi N US Hwy 78. St. Clair County: TU 26026 (1), Beaver Cr., 4 mi S Ashville, US Hwy 231; TU 26015 (11), Broken Arrow Cr., 9.0 mi N Pell City, US Hwy 231; TU 26037 (21), Muckleroy Cr., trib. to Big Canoe Cr., 4.0 mi NW Ashville, US Hwy 231. Cherokee County: TU 26067 (10), Mills Cr., trib. to Chattooga R., 3 mi ENE Chesterfield; TU 40768 (1), Terrapin Cr., 7.8 mi N Piedmont, Ala Hwy 9. COOSA RIVER SYSTEM, GEORGIA. Floyd County: TU 32754 (42), Cave Springs Cr., trib. to Cedar Cr., Cave Springs, Rolater Park; TU 7865 (24) and TU 26111 (7), Silver Cr. at town of Silver Creek; TU 25962 (3) and TU 26118 (6), Spring Cr., trib. to Etowah R., 5 mi E Rome, US Hwy 411. Chattooga County: TU 26081 (15), trib. to Chattooga R., 5 mi SW Lyerly, Ga Hwy 114; TU 33358 (6), Harrisburg Cr., 10.5 mi N Menlo, Ga Hwy 337; TU 34983 (16), trib. to Chattooga R., 5.3 mi W Lyerly; TU 26104 (8), trib. to Chattooga R., Lyerly, Ga Hwy 114; TU 27565 (2), spring trib. to Chattooga R., 0.2 mi E Alabama/Georgia state line, 5.3 mi W Lyerly; UT 91.1928 (15), West Fork Armuchee Cr., Ga Hwy 201, 8.9 mi NE junction US Hwy 27. Walker County: TU 40678 (29), Duck Cr., 1.3 mi NE Center Post, Ga Hwy 337; TU 27574 (10), Cane Cr., trib. to Chattooga R., 2.5 mi E Point, 8.3 mi S Lafayette; TU 40688 (69), Duck Cr., 6.8 mi SW Lafayette off Ga Hwy 337, 0.2 mi E Bronco; UT 91.1929 (17), Cane Cr., US Hwy 27, 5.5 mi S junction with Ga Hwy 193, Lafayette. Bartow County: TU 7393 (3), Little Pinelog Cr., 2 mi N White, US Hwy 411; TU 12076 (11), Cedar Cr., trib. to Pinelog Cr., 0.3 mi W Folsom, Ga Hwy 140. Gordon County: TU 35027 (31), Rocky Branch, trib. to Johns Cr., 10.5 mi W Calhoun, Ga Hwy 156. Murray County: CU 24908 (20) and TU 37543 (7), Rock Cr., trib. to Coosawattee R., 1.5 mi S Chatsworth, US Hwy 411; TU 27969 (3), Holly Cr., 0.5 mi E Chatsworth, US Hwy 76; TU 7328 (3), Rock Cr., trib. to Holly Cr., Ramhurst; UT 91.13 (3), Holly Cr., 3 mi E Eton; UT 91.1685 (13), Conasauga R., 0.5 river mile S Tennessee/Georgia state line; UT 91.1689 (27), Conasauga R., Ga Hwy 2; TU 121091 (1), Conasauga R., 0.9 mi W Gregory, Ga Hwy 225. Pickens County: TU 40722 (27) and TU 38352 (7), Talking Rock Cr., 13.6 mi S Ellijay, Ga Hwy 5. COOSA RIVER SYSTEM, TENNESSEE. Bradley County: TU 65932 (12) and TU 121066 (15), Conasauga R., 12.9 mi SE Cleveland, Tenn Hwy 74; UT 91.280 (33), Mills Cr. at Tennessee/Georgia state line, E Red Clay. Polk County: UT 91.147 (21), Minnewauga Cr. near mouth; UT 91.248 (27), Conasauga R. at Boanerges Church bridge; UT 91.2836 (6), Old Fort Cr. near US Hwy 411.

Acknowledgments

Study materials and distributional records of the three snubnose darters treated herein have been accumulating over the years, due to the efforts of a number of past Tulane graduate students and fellow faculty. They are in alphabetical order: Robert C. Cashner, Glenn H. Clemmer, John DeAbate, the late Gerald E. Gunning, Rudolph J. Miller, John S. Ramsey, and Bruce A. Thompson. We are also indebted to two anonymous reviewers. We are apprecia-

tive of the loan of material, collection data, and courtesies extended to us by Richard L. Mayden and Bernard R. Kuhajda, University of Alabama; Maurice F. Mettee and Patrick E. O'Neil, Geological Survey of Alabama; Henry L. Bart, Jr., Auburn University; B. J. Freeman, University of Georgia; and J. Malcolm Pierson, Alabama Power Company. We are most appreciative of the efforts of the many students at these various institutions.

We are greatly indebted to a number of individuals who have contributed significantly to our study by collecting, making observations, and taking photographs. Jeanne E. Suttkus helped collect and photograph snubnose darters in the late 1960s and early 1970s. More recently, we have had a tremendous amount of assistance and donations of slides by J. Malcolm Pierson, Maurice F. Mettee, Patrick E. O'Neil, Henry L. Bart, Jr., and B. J. Freeman.

Literature Cited

Bailey, R. M. and D. A. Etnier. 1988. Comments on the subgenera of darters (Percidae) with descriptions of two new species of *Etheostoma* (*Ulocentra*) from southeastern United States. Misc. Publ. Mus. Zool. Univ. Michigan 175: 1–48.

Boschung, H. T., Jr. 1961. An annotated list of fishes from the Coosa River system of Alabama. Amer. Midl. Nat. 66: 257–285.

Bouchard, R. W. 1977. *Etheostoma etnieri*, a new percid fish from the Caney Fork (Cumberland) River system, Tennessee, with a redescription of the subgenus *Ulocentra*. Tulane Stud. Zool. Bot. 19: 105–130.

Burr, B. M. and R. C. Cashner. 1983. *Campostoma pauciradii*, a new cyprinid fish from southeastern United States, with a review of related forms. Copeia 1983: 101–116.

Carney, D. A. and B. M. Burr. 1989. Life histories of the bandfin darter, *Etheostoma zonistium*, and the firebelly darter, *Etheostoma pyrrhogaster*, in western Kentucky. Ill. Nat. Hist. Surv. Biol. Notes 134: 1–16.

Etnier, D. A. and R. M. Bailey. 1989. *Etheostoma* (*Ulocentra*) *flavum*, a new darter from the Tennessee and Cumberland river drainages. Occ. Pap. Mus. Zool. Univ. Michigan 717: 1–24.

Fowler, H. W. 1945. A study of the fishes of the southern Piedmont and Coastal Plain. Monogr. Acad. Nat. Sci. Philadelphia 7: 1–408.

Hubbs, C. L. and K. F. Lagler. 1958. Fishes of the Great Lakes region. Cranbrook Inst. Sci. Bull. 26 (i–xiii, 1–213 pp.).

Jenkins, R. E. 1976. A list of undescribed freshwater fish species of continental United States and Canada, with additions to the 1970 checklist. Copeia 1976: 642–644.

Kuehne, R. A. and R. W. Barbour. 1983. The American Darters. Univ. Kentucky Press, Lexington, 201 pp.

O'Neil, P. E. 1981. Life history of *Etheostoma coosae* (Pisces: Percidae) in Barbaree Creek, Alabama. Tulane Stud. Zool. Bot. 23: 75–83.

Page, L. M. 1983. Handbook of Darters. T. F. H. Publications, Inc., Neptune City, N.J., 271 pp.

Page, L. M. and B. M. Burr. 1982. Three new species of darters (Percidae, *Etheostoma*) of the subgenus *Nanostoma* from Kentucky and Tennessee. Occ. Pap. Mus. Nat. Hist. Univ. Kansas 101: 1–20.

Page, L. M. and R. L. Mayden. 1981. The life history of the Tennessee snubnose darter, *Etheostoma simoterum*, in Brush Creek, Tennessee. Ill. Nat. Hist. Surv. Biol. Notes 117: 1–11.

Ramsey, J. S. 1976. Freshwater fishes. *In*: Endangered and threatened plants and animals of Alabama. Bull. Alabama Mus. Nat. Hist. No. 2 (pp. 53–65).

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada (4th ed.). Amer. Fish. Soc. Spec. Publ. 12 (pp. 1–174).

Sizemore, D. R. and W. M. Howell. 1990. Fishes of springs and spring-fed creeks of Calhoun County, Alabama. Proc. Southeastern Fishes Council 22: 1–6.

Smith-Vaniz, W. F. 1968. Freshwater Fishes of Alabama. Auburn Univ. Agric. Exper. Sta.

Stiles, R. A. and D. A. Etnier. 1971. Fishes of the Conasauga River drainage, Polk and Bradley Counties, Tennessee. J. Tennessee Acad. Sci. 46: 12–16.

Stiles, R. A., M. J. Larkin, and J. Oliver. 1987. Comparison of the reproductive behavior of members of the subgenus *Ulocentra* (Percidae, *Etheostoma*) with that of *Etheostoma zonale*. Amer. Soc. Ichthyol. and Herpetol., 67th Annual Meeting (abstract).

MCZ
LIBRARY
FEB 01 1993
HARVARD
UNIVERSITY

TULANE STUDIES IN
ZOOLOGY AND BOTANY

Volume 28, Number 2 November 16, 1992

A SYSTEMATIC STUDY OF THE PALEOTROPICAL GENUS *ANTIRHEA* (RUBIACEAE: GUETTARDEAE)

SHU-MIAW CHAW
INSTITUTE OF BOTANY, ACADEMIA SINICA
NANKANG, TAIPEI, TAIWAN 11529
REPUBLIC OF CHINA

AND

STEVEN P. DARWIN
DEPARTMENT OF ECOLOGY, EVOLUTION, AND ORGANISMAL BIOLOGY
TULANE UNIVERSITY
NEW ORLEANS, LOUISIANA 70118

Tulane
University
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY AND BOTANY

ISSN 0082-6782

Department of Ecology, Evolution, and Organismal Biology
Tulane University, New Orleans, Louisiana, 70118

ARTHUR L. WELDEN, Editor

INFORMATION FOR AUTHORS

Manuscripts dealing with all aspects of ecology, evolution, and systematic biology are encouraged. All manuscripts are reviewed.

Page charges are assessed at the rate of $45 per page. Some limited financial assistance from the George Meade Memorial Fund is available if authors are unable to meet these charges.

Style of manuscript should follow guidelines appearing in the Council of Biology Editors Style Manual.

Manuscript (with abstract) must be typed on good quality 8.5 x 11 inch paper, double-spaced throughout (including Literature Cited, figure captions, footnotes, and tables). All pages must have 1 inch margins on all sides. Dot-matrix printing is not acceptable; do not justify right-hand margins. Do not hyphenate words at ends of lines. Last name(s) of author(s) should appear on each page with page number; this includes tables and figure captions.

Lettering used in figures must be easily read after reduction to our page size. Photographs (halftones) should be made for no or little reduction.

The original and three copies of the manuscript, along with figures, should be submitted.

Prospective authors should request a copy of the detailed guidelines for manuscript preparation (including footnotes, typefaces, literature and specimen citation, and dimensions of figures) from the Editor at the above address.

EXCHANGES AND STANDING ORDERS

Tulane Studies in Zoology and Botany is available for exchange with institutions publishing comparable series. Otherwise, standing orders are accepted, with issues priced individually (foreign postage extra). A price list for back issues is available on request. Remittances should be made payable to Tulane University.

A SYSTEMATIC STUDY OF THE PALEOTROPICAL GENUS *ANTIRHEA* (RUBIACEAE: GUETTARDEAE)

SHU-MIAW CHAW
Institute of Botany, Academia Sinica
Nankang, Taipei, Taiwan 11529
Republic of China

STEVEN P. DARWIN
Department of Ecology, Evolution, and Organismal Biology
Tulane University
New Orleans, Louisiana, 70118

ABSTRACT

Antirhea (Rubiaceae, tribe Guettardeae) is a genus of 36 species distributed from Madagascar and the Mascarene Islands eastward through Malesia to the Philippines, southern China, tropical Australia, Melanesia, New Caledonia, Fiji, and Samoa. Twelve species and one variety are described as new, and eleven new combinations are made. Three subgenera are recognized. *Antirhea* species are trees or shrubs with dioecious flowers arranged in cymes (or these frequently reduced to solitary flowers in pistillate plants), corollas with three or four imbricate lobes, and the same number of epipetalous stamens. The pollen is semitectate and inaperturate or 1-porate. Ovaries have two to twelve locules with solitary, pendulous ovules. The drupaceous fruits have fused pyrenes and persistent calyces. A close relationship among *Antirhea*, *Timonius*, and *Bobea* is suggested. New World taxa sometimes assigned to *Antirhea* are here tentatively placed in *Stenostomum*. Character evolution and geographical distribution are discussed and keys are provided to all infrageneric taxa.

SIZE AND DISTRIBUTION

As interpreted here, *Antirhea* Juss. includes 36 paleotropical species extending from Madagascar and the Mascarene Islands eastward to the Malay Peninsula, Borneo, the Celebes, Moluccas, Lesser Sunda Islands, New Guinea, tropical Australia, the Solomon Islands, and the South Pacific, with a northern extension to southern China and the Philippines. Our circumscription includes the segregate genus *Guettardella* Benth., but excludes all (roughly twenty) New World species ascribed to *Antirhea* by Urban (1899, 1912, 1915, 1923, 1928, 1929, 1932), Standley (1934), and other authors who followed Hooker's (1873) broad generic concept. All of those neotropical taxa are most likely assignable to *Stenostomum* Gaertner (the genus under which many of them were originally described) or to *Pittoniotis* Griseb., but firm conclusions will require more study. In the following discussion, and unless otherwise indicated, the generic name *Antirhea* refers only to the paleotropical species.

Antirhea was treated by Merrill (1923) for the Philippines, by White (1946) for Australia, by Verdcourt (1983) for the Mascarene Islands, and recently by

Jansen (1984) for the paleotropics generally. The genus includes frutescent to arborescent species of Rubiaceae with dioecious flowers arranged in fundamentally dichasial cymes (or these frequently reduced to solitary flowers in pistillate plants); imbricate corollas with three or four lobes and the same number of stamens; semitectate, inaperturate to 1-porate pollen; ovaries with usually 2—12 locules; drupaceous fruits with united pyrenes; and persistent calyces and floral bracts.

In contrast, the New World species of *Stenostomum* and *Pittoniotis* apparently have hermaphrodite (rarely polygamous) flowers and colpate pollen. Furthermore, their leaf venation differs from that of *Antirhea*, where veinlets tend to be oriented at right angles to the midrib or to adjacent secondary veins (Bremekamp, 1959). Elucidation of interspecific relationships in *Stenostomum* and *Pittoniotis* will require a separate study and comparison with other New World Guettardeae, especially *Guettarda*.

Antirhea species are reported from a variety of habitats, such as coastal scrubs and thickets, savanna forest, disturbed roadsides, ravines, stream banks, secondary forests, lowland or montane rain forests, and swamps (some collections of *A. inconspicua*). Species range from near sea level to 1800 meters elevation. Several species grow (exclusively?) on limestone rocks or soils derived from limestone (*A. atropurpurea*, *A. bombysia*, *A. buruana*, *A. hexasperma*, *A. inconspicua*, and *A. multiflora*). Two taxa seem confined to coastal or subcoastal habitats (*A. madagascariensis* and *A. ovatifolia*). The genus is of little use economically, although the generic name, derived from Greek (against + flow), refers to a use of *A. borbonica* to stop hemorrhage.

Prior Studies

In 1789, de Jussieu described *Antirhea* from a collection made by Commerson on the island of Réunion. De Jussieu considered the genus characterized by 4-merous flowers, included, subsessile anthers, and calyx-crowned drupes with two united, bony pyrenes; he suggested an alliance with *Psychotria* L. and *Malanea* Aublet. In March of 1791, Lamarck illustrated the same species, later naming it *Malanea verticillata* Desr. when the accompanying text appeared in 1792. However, Lamarck's species name was predated by *Antirhea borbonica*, published by Gmelin (Sept.-Nov., 1791) and based on de Jussieu's generic description. *Malanea bifurcata* Desrousseaux, from the Mascarene Islands, was described in 1792 but misattributed to the West Indies; this species was later transferred to *Antirhea* by J. D. Hooker in 1873.

In the meantime, de Candolle (1830) proposed the name *A. frangulacea*, based on a collection from Mauritius, expanding de Jussieu's original generic concept by including specimens with 3-branched styles and 3-seeded fruits. De Candolle was the first to relate *Antirhea* (then comprising only two species) to the Caribbean *Stenostomum* Gaertner, remarking on their similar inflorescences, but pointing out the 5-merous flowers of the latter genus. In describing *A. dioica* (= *A. borbonica* Gmelin) from Mauritius, De Candolle was also the first to recognize *Antirhea* as including dioecious species.

Richard (1830), perhaps influenced by de Jussieu's (1789, 1791, 1820) remarks as to a close affinity between *Antirhea* and *Malanea* Aublet, combined the two genera under the latter name, but that circumscription was not subsequently accepted. *Malanea* species, as now usually interpreted, occur only in the neotropics, have a usually scandent habit, valvate corolla lobes, spiciform to paniculate inflorescences, villose corolla throats, exserted stamens, and separate pyrenes.

Endlicher (1838, 1841) and Lindley (1846, 1847, 1853) listed the dubious genus *Neuropora* Commers. as a synonym of *Antirhea* without comment. The name was taken from de Candolle (1830), who found it in Thouin's herbarium and considered it a synonym of *A. dioica* (= *A. borbonica*).

Bentham's (1852) *Guettardella*, based on a Champion collection from Hong Kong, initially included two species: the type, *G. chinensis* (= *Antirhea chinensis* (Champ. ex Benth.) Hook. f.), and *G. philippinensis* (= *A. philippinensis* (Benth.) Rolfe). He later (Bentham, 1867) described two Australian taxa, *Antirhea tenuiflora* (with usually 3-seeded fruits) and a third *Guettardella* species, *G. putaminosa* (F. v. Muell.) Benth. (with 4- to 5-seeded fruits), noting that *Antirhea* is "perhaps too closely allied . . . to . . . *Guettardella*." He distinguished the genera on the basis of a 2-celled ovary in *Antirhea*, the cells more numerous in *Guettardella*. Recently, Jansen (1984) restricted *Antirhea* to two Mascarene species, assigning all other Old World *Antirhea* species to *Guettardella*. His generic distinction was founded largely on floral sexuality, number of flowers per inflorescence, number of ovary cells, and geographical distribution.

J. D. Hooker (1873) referred *Stenostomum* and *Guettardella* to *Antirhea*, amplifying the generic characters (such as number of floral parts and locules per ovary). *Stenostomum* and *Antirhea* were likewise regarded as congeneric by Schumann (1891), Standley (1934), Bremekamp (1952, 1959), Pray (1953), Steyermark (1967, 1974), and Airy Shaw (1973), among others. Consequently, *Antirhea* became known as a trans-Pacific genus. However, *Stenostomum* (sensu typi), marked by ebracteolate inflorescences, monoecious, heterostylous, and (4-) 5-merous flowers, semitectate-reticulate and distinctly 3-colpate pollen (Figure 1a), two-celled ovaries, and fruits with 2 (—10) fused pyrenes, seems to us better regarded as a separate genus.

Baillon (1880) merged *Antirhea* (and other genera) into *Guettarda*, but the latter genus, with about 80 mainly neotropical species (Airy Shaw, 1973), is readily distinguishable from *Antirhea* by its deciduous calyx. Baillon's very broad concept of *Guettarda* has never been accepted.

Another neotropical genus, *Pittoniotis* Griseb., with a single species, *P. trichantha*, distributed from Panama to northeastern Colombia and Venezuela, was assigned to *Antirhea* by Hemsley (1881), a disposition accepted by, e.g., Schumann (1891), Airy Shaw (1973), and Dwyer (1980). The genus was maintained by Standley (1934), Pray (1953), Steyermark (1974), and Standley and Williams (1975). Primary differences from *Antirhea* are the paniculate cymes, perfect flowers, villose corolla lobes, and long-exserted stamens. Pray (1953) noted that *Pittoniotis* is unusual among Guettardeae in that sclerenchyma is absent in the leaf veinlets. We find the pollen of *Pittoniotis* to be decidedly tectate-perforate and 3-colpate (Figure 1b).

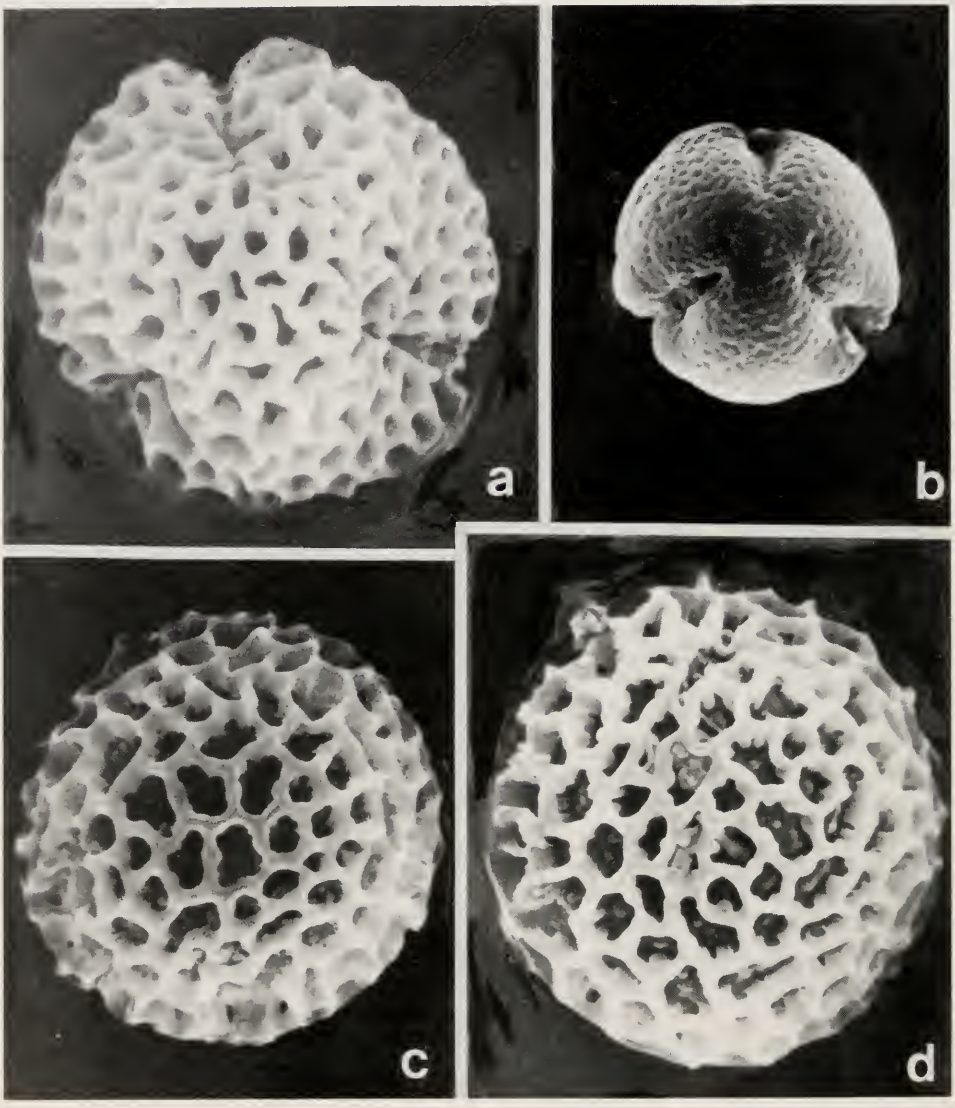


Figure 1. Scanning electron micrographs of acetolyzed pollen grains from representative species of *Stenostomum*, *Pittoniotis*, and *Antirhea*, all × 3000. a. *S. lucida* (*Clemente 3217*). b. *P. trichantha* (*Pitter 6588*). c. *A. borbonica* var. *borbonica* (*Ayers* s.n.). d. *A. chinensis* (*Tso 21712*).

Useful Features

Habit—All species of *Antirhea* are woody. *Antirhea borbonica*, *A. megacarpa*, *A. nova-britanniensis*, *A. schmutzii*, and *A. tenuiflora*, all confined to humid, montane or lowland rain forests, are tall trees (to 33 meters). Other species, largely recorded from low altitudes and less moist (even semiarid) regions are generally shrubs or trees to 10 meters tall. The tree habit is likely derived from suffrutescence in the genus. When field notes are available (mostly for collections from China, New Guinea, and Queensland) the boles are reported as straight and

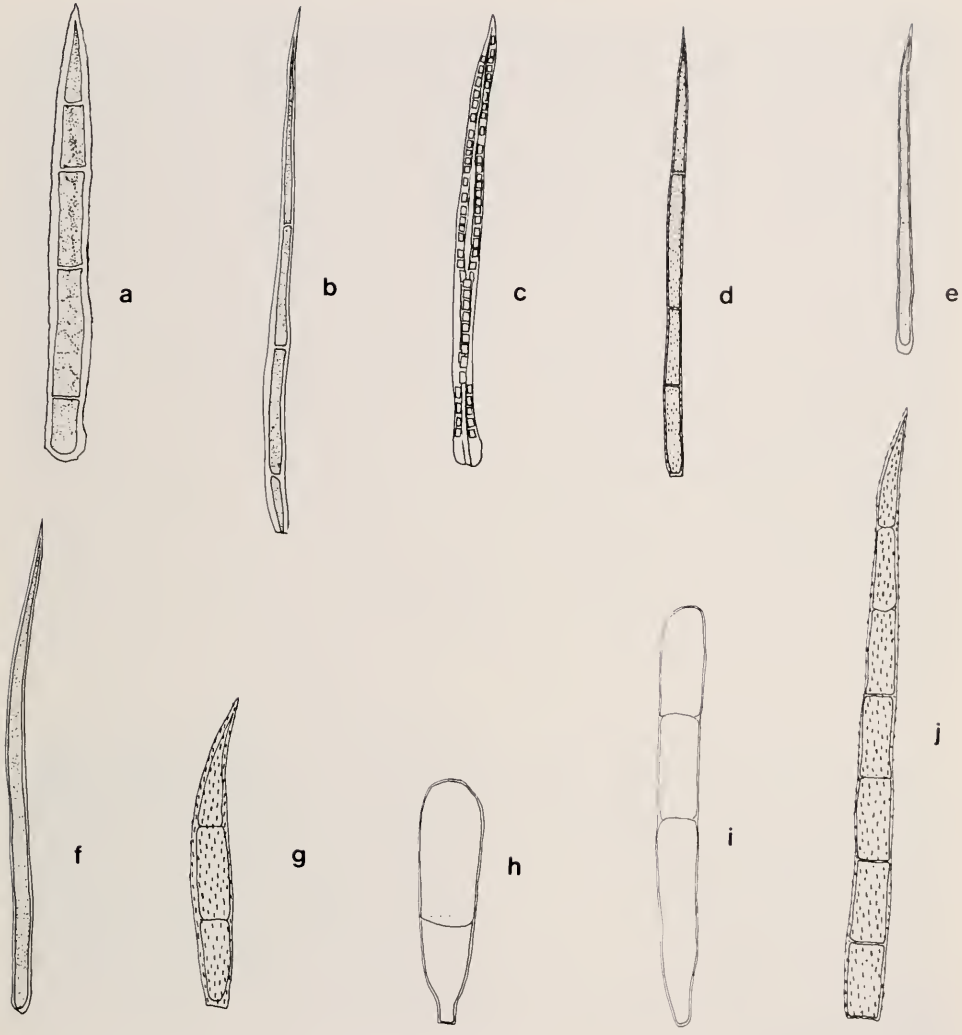


Figure 2. Trichomes from representative species of *Antirhea*. a—e. *A. chinensis* (*Wright 217* ♂). a. Multicellular trichome with scabrous wall, from branchlet, × 250. b. Multicellular trichome with smooth wall, from adaxial surface of stipule, × 100. c. Crystalliferous trichome from adaxial surface of leaf blade, showing 2 files of crystals in the thick trichome wall, × 250. d. Multicellular trichome from adaxial surface of leaf blade, × 100. e. Unicellular trichome from adaxial surface of corolla tube, × 100. f—g. *A. borbonica* var. *borbonica* (*Schlieben 10942* ♂). f. Unicellular trichome with smooth wall, from adaxial surface of corolla tube, × 100. g. Multicellular trichome with scabrous wall, from abaxial surface of corolla tube, × 10. h—j. *A. ovatifolia* (*Brass 19599* ♂), all × 100. h–i. Multicellular, clavate trichome, from domatium. j. Multicellular trichome with scabrous wall, from abaxial surface of leaf blade.

distinct, the outer bark as "thin," "flaky," "smooth," or "very finely pustular," and pale brown, gray-brown, or dark brown to black, the inner bark as white, pinkish, cream, yellowish brown, or yellow, darkening on exposure.

Trichomes—Antrorse, multicellular hairs (composed of 2—5 cells of variable size) with acute apices are always present on the outer surfaces of corolla tubes

(Figure 2g), and similar hairs are usually present on calyces and other inflorescence parts. In *Antirhea borbonica* and *A. madagascariensis* the inflorescences, except the corolla tubes, are usually sparsely puberulent to glabrous. Wherever branchlets, leaves, or stipules are pubescent, their indument is characterized by multicellular trichomes. Such hairs have smooth (mainly on stipule interiors) to minutely or strikingly scabrous walls (Figure 2a-b, d, j). Unicellular hairs with smooth walls are found on corolla tube interiors (Figure 2e-f). Some unicellular hairs have thick walls in which small angular crystals are deposited in two files along the trichome length (Figures 2c; 3a). These "crystal-hairs" (Solereder, 1908) or "crystaliferous trichomes" (Pray, 1953) are disposed among the multicellular trichomes on leaves (particularly abaxial surfaces), on outer surfaces of corolla tubes and calyces, and on the ovaries. Solereder states that the hairs are "a very characteristic feature of the tribe Guettardeae," and Bremekamp (1952, 1966) employed the character to delimit the tribe.

Among the Old World species of *Antirhea*, multicellular, clavate trichomes are sometimes present on the abaxial margins of overlapped corolla lobes. Occasionally, similar trichomes (Figure 2h-i) are scattered among the usually acute hairs associated with domatia (*Antirhea chinensis* and *A. ovatifolia*) and the abaxial base of the calyx tube (*A. livida*). Scabrous to papillose, unicellular trichomes are present on the adaxial surfaces of corolla lobes of all species, and sometimes also on the style (*A. chinensis*, *A. ioensis*, *A. paxillata*, *A. rhamnoides*, *A. smithii*, and *A. talaudensis*). Colleters are variously distributed over adaxial surfaces of stipules.

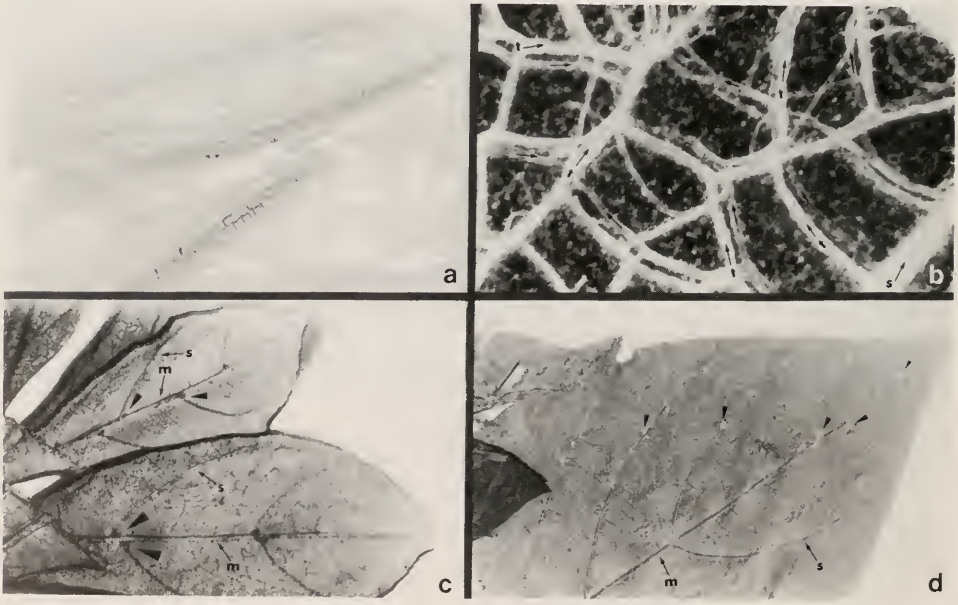


Figure 3. Leaf blade characters in *Antirhea* species. a. Unicellular trichomes from abaxial leaf-blade surface of *A. tayabensis* (*BS 28869*) showing crystals in two files along trichome length, × 250. b. Cleared leaf of *A. schmutzii* (*Schmutz 4820*) showing spirally sculptured fibers (s) running parallel with conducting tissues (arrows direct toward midrib), × 60. c. Adaxial leaf blade surface of *A. borbonica* var. *borbonica* (*Puff 800822-1/1*) showing dome-like domatia (arrows), × 1. d. Domatia (arrows) of tufted hairs in axils of secondary and tertiary veins in *A tayabensis* (*BS 28869*) × 1.65.

Crystals—Crystal sand in abaxial epidermal cells of leaf blades was observed only in species from the Indian Ocean islands. Such crystals form circular or elongate clusters over the leaf venation. Their presence is likely a derived character in *Antirhea*, but they are also known in some species of *Timonius*.

Crystals embedded in the walls of unicellular trichomes are consistently present in all *Antirhea* species. Pray (1953) described the crystals as occupying the cell lumen, but that interpretation results when the hairs are viewed from the side and the crystals appear to be superimposed. Bremekamp (1966) mentions that the crystals are calcium oxalate. No raphides were observed.

Leaves and stipules—The simple, entire leaves are usually opposite at each node, except in *Antirhea borbonica* and *A. madagascariensis* where the leaves are regularly in whorls of three. Whorled leaves are also sometimes found in *A. inconspicua*, *A. microphylla*, and *A. talaudensis*. The leaf blades are membranaceous to thin-chartaceous or coriaceous; subcoriaceous to coriaceous blades are mainly restricted to species from the eastern and western edges of the generic distribution—in species from the Indian Ocean (*A. borbonica*, *A. madagascariensis*), and from Flores, Ceram, New Guinea and adjacent islands, to Fiji; available specimen notes did not suggest a correlation between leaf blade texture and habitat. The stomata, confined to lower leaf surfaces, are paracytic. Petioles are somewhat 3-angled to subterete at base, distally subterete to semiterete, adaxially canaliculate, and often winged by the blade.

Nodal and petiolar anatomy was examined in revived herbarium specimens sectioned by hand. Petioles were sectioned near the base, middle, and distal end using Soladoye's (1982) sectioning and staining method. The examined species were found to exhibit two different patterns of nodal and petiolar vascular anatomy which, based on Howard's (1962, 1979) classification, may be described as follows:

1. Node with one trace and one gap associated with each leaf, the trace simple, U-shaped, with rib traces developed in the petiole (Figure 4i-l). This pattern characterizes subgenus *Guettardella*. At the level of the node, the vascular trace is single and continuous, forming a deep arc, which can be seen clearly from leaf scars. At the petiole midpoint and distal region, the vascular arc becomes more shallow, its ends more invaginated or not, and two lateral rib traces become apparent.

2. Node with three traces and three gaps associated with each leaf, the bundles free (Figure 4a-d, e-h). This pattern is found in subgenera *Antirhea* and *Mesocarpa*. In the petiole, the abaxial trace is similar in shape to the vascular arc of the previously described pattern; the other two traces (much smaller and more terete) are located at both lateral corners of the petiole. There are two (rarely only one in *A. smithii*) additional terminal rib traces apparent near the base of the leaf blade (e.g., *A. megacarpa*) (Figure 4h).

In petioles of all species examined, the radially arranged xylem vessels are abaxially associated with phloem cells. Spirally sculptured fiber cells (when present) are scattered along the adaxial and abaxial sides of the vascular arc (e.g., *Antirhea smithii*, Figure 5a-c; *A. ioensis*, Figure 5d-f) or aggregated at each end of the vascular arc (*A. edanoi*, Figure 5g-h). Similar fibers are common at the adaxial

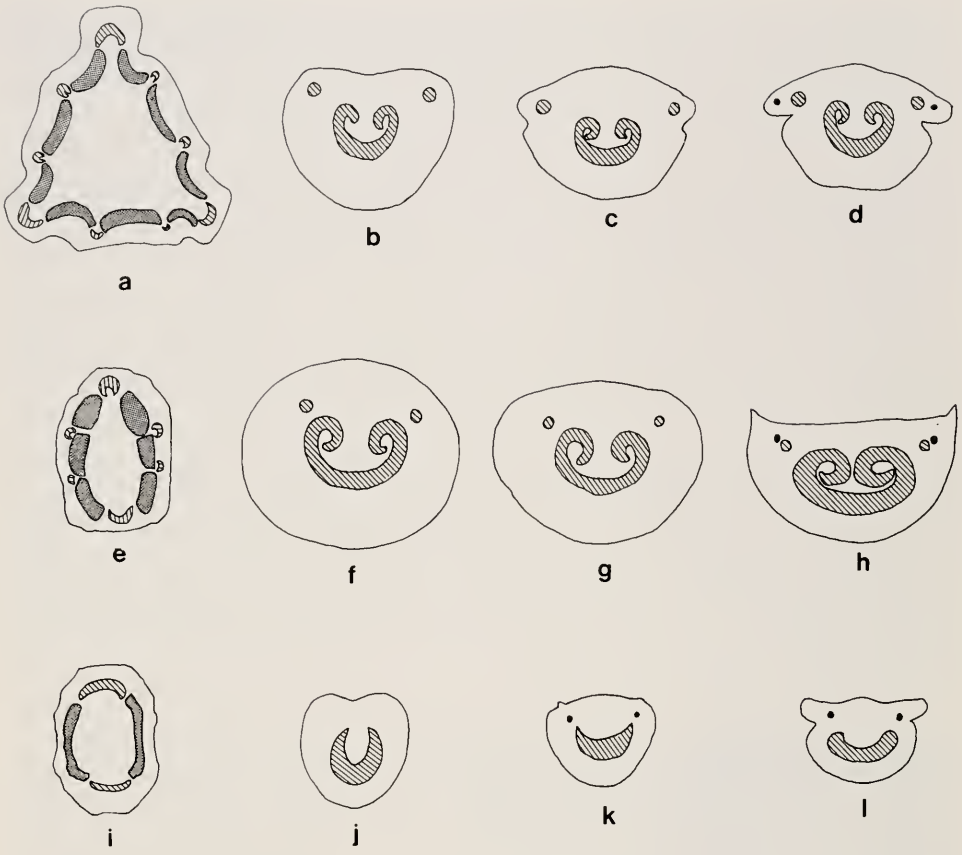


Figure 4. Selected nodal and petiolar vascular patterns from representative species of *Antirhea*. a—d. *A. borbonica* var. *borbonica* (*St. John 26499* ♀). a. Cross section of node with whorled leaves showing for each leaf 3 traces from 3 gaps. b–d. Successive sections of petiole from base, mid-portion and distal end, showing curved vascular arc and lateral rib traces. e—h. *A. megacarpa* (*NGF 1235* ♀) e. Cross section of node with opposite leaves showing for each leaf 3 traces from 3 gaps. f–h. Successive sections of petiole from base. i—l. *A. chinensis* (*Lau 3150* ♂) i. Cross section of node with opposite leaves showing for each leaf 1 trace from 1 gap. j–l. Successive sections of petiole from base, mid portion and distal end respectively, showing curved vascular arc and rib traces developed at midpoint of petiole. Cross-hatched area = disrupted vascular cylinder; slashed area = leaf trace; solid area = lateral rib trace.

and abaxial sides of the smaller petiolar traces, becoming more abundant and enclosing the traces completely toward the distal portion of the petiole. The petiolar vascular pattern of Old World *Antirhea* species might be correlated with habit: subgenera *Antirhea* and *Mesocarpa* (except *A. bifurcata*) are trees, while in subgenus *Guettardella* shrubs are prevalent.

Interpetiolar stipules are conspicuous in terminal buds, and usually caducous or sometimes persistent at the most distal nodes (*Antirhea benguetensis*, *A. microphylla*, *A. ovatifolia*). The stipules may be valvate or slightly imbricate or distinctly imbricate and conduplicate. All species from the Indian Ocean region have valvate stipules, whereas species from other regions seem to exhibit no geographical correlation with respect to stipule aestivation. The adaxial surfaces of

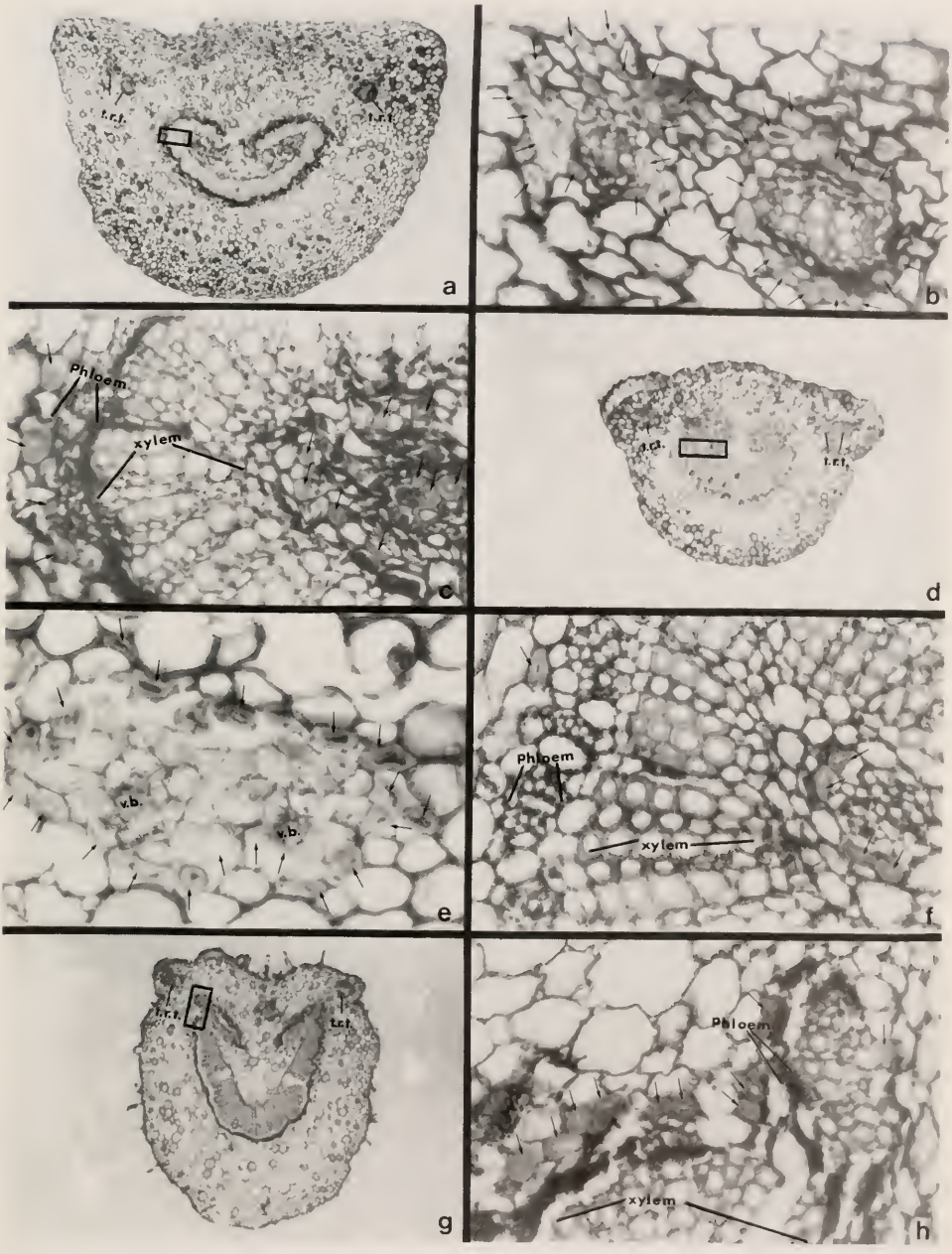


Figure 5. Cross sections of petioles of selected *Antirhea* species. Arrows point to spirally sculptured fibers. a—c. *A. smithii* (*Smith 1347*) a. Distal end of petiole, × 52. b. Enlarged portion of the left rib trace (r.t.) shown in Figure a, × 520. c. Enlarged portion of square area in Figure a, showing sculptured fibers on both sides of vascular arc, × 520. d—f. *A. ioensis* (*McMillan 5048*). d. Mid-portion of petiole, × 52. e. Enlarged portion of right rib trace seen in Figure d, × 520. f. Enlarged portion of square area in Figure d, showing scattered fibers, × 520. g—h. *A. edanoi* (*BS 43943*). g. Distal end of petiole, × 52. h. Enlarged portion of left vascular arc, showing fibers aggregated at both ends of the vascular arc, × 520. v.b. = vascular bundle; t.rt. = terminal rib trace.

stipules are constantly pubescent (but sometimes only near or at base), and are invested with scattered, finger-like colleters typical of many Rubiaceae (see Robbrecht, 1988). Basally sheathing stipules (fused intrapetiolary) are limited to *A. buruana* and *A. hexasperma* (eastern Borneo and the Celebes to Ambon).

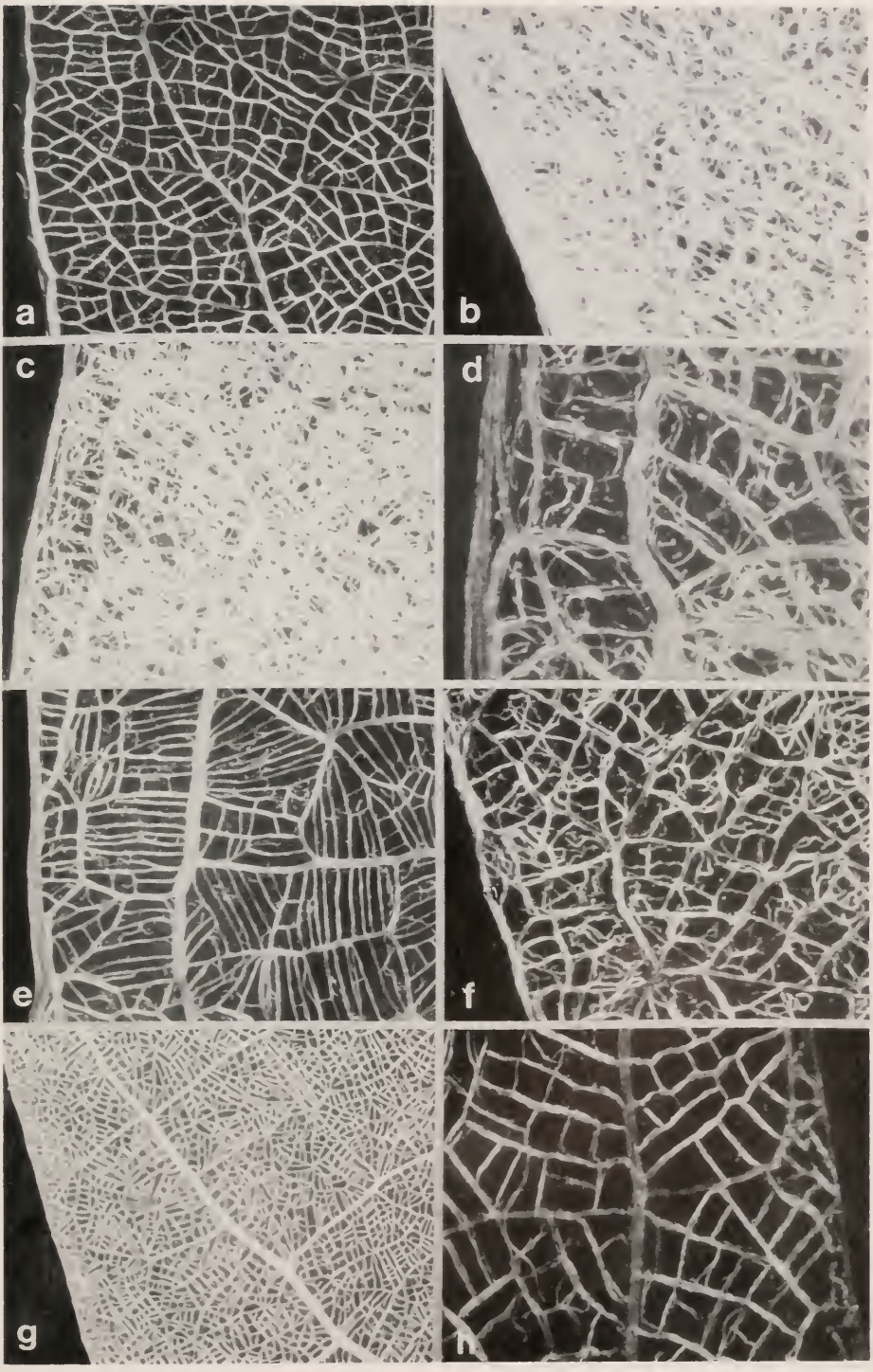
Venation—In order to study venation patterns, we cleared leaves from herbarium specimens according to the method of O'Brien and Teichman (1974); the cleared leaves were permanently mounted on glass slides and examined under polarized light. In mature leaves, the major venation is eucamptodromous (Hickey, 1973, 1979), with a prominent costa (midrib) and several pairs of pinnately divergent secondary veins, these gradually diminishing and terminating near the margin. In addition to the secondary veins, "intermediate veins" (Foster, 1950) or "intersecondary veins" (Hickey, 1973, 1979) may emerge from the costa. These intersecondary veins are entirely bounded within the "intersecondary panels" (cf. Pray, 1959) delimited by the secondary veins. In specimens studied, tertiary veins and veinlets frequently are not distinguishable from one another, or the tertiary veins are sometimes prominent in the intersecondary panels. All intersecondary venation (exclusive of the intersecondary veins themselves) is here referred to as "minor venation" (cf. Pray, 1959).

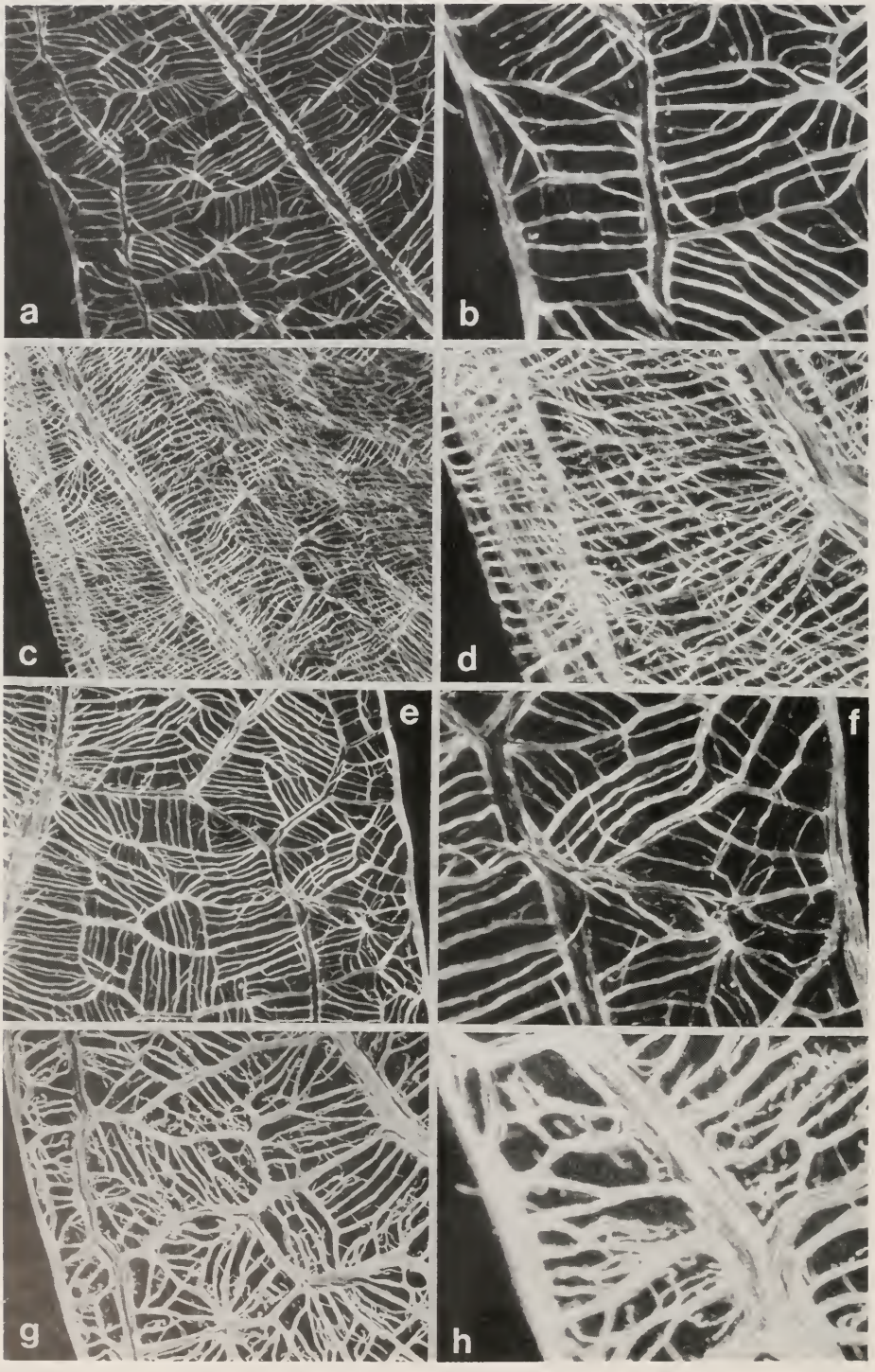
In species examined, the conducting tissues are surrounded by spirally sculptured fibers. Solereder (1908) noted similar sclerenchymatous fibers in other rubiaceous genera. In our species they are usually closely associated with the conducting tissues, or occasionally branch from them and run parallel with the veinlets (e.g., *Antirhea schmutzii*, Figure 3b), thus appearing as a second network of veinlets. In *A. madagascariensis* and two New Caledonian species (*A. ioensis* and *A. rhamnoides*), the fibers are wide (seen in surface view in cleared leaves) relative to the minor venation, and prominent (Figure 6b; 8b).

The smallest subdivisions of the mesophyll enclosed by veinlets (i.e., the areoles) are consistently well developed in all paleotropical *Antirhea* species. Free veinlets ending within areoles are infrequent, but regularly present in the Indian Ocean species (*A. bifurcata*, Figure 6a; *A. borbonica*, Figure 6c-d; *A. madagascariensis*, Figure 6b) and one South Pacific species (*A. smithii*, Figure 6f), and often in two Australian species (*A. putaminosa* and *A. tenuiflora*, Figure 8e-f). Areoles with included, free-ending veinlets tend to be square or irregularly elongate (the above-mentioned Australian taxa). The free-ending veinlets are devoid of accompanying spirally sculptured fibers, at least toward the distal end.

In most *Antirhea* species, the areoles are elongate and often lie parallel with one another in groups ("lineolate" veinlets); the groups are usually arranged to form a reticulate pattern. Although the actual shapes of areoles are extremely variable, the general tendency toward elongation is often well expressed. However, elongate areoles are wanting in *Antirhea borbonica* (Figure 6c-d) and *A. madagascariensis* (Figure 6b), and rare in *A. bifurcata* (Figure 6a), *A. schmutzii* (Figure 6g-h), *A. anodon*, *A. nova-britanniensis*, and *A. smithii* (Figure 6f).

Figure 6. Leaf venation patterns in selected species of *Antirhea*. a. *A. bifurcata* (*Balfour* s.n.), × 8. b. *A. madagascariensis* (*Capuron 27755-SF*), × 8. c. *A. borbonica* var. *borbonica* (*Puff 800822-1/1*), × 8. d. Same, × 20. e. *A. megacarpa* (*Brass 946*), × 8. f. *A. smithii* (*Smith 1347*), × 8. g. *A. schmutzii* (*Schmutz 4820*), × 8. h. Same, × 20.


a
b
c
d
e
f
g
h


a
b
c
d
e
f
g
h

A lineolate minor venation of distinctly elongate areoles is strongly displayed in most of the species assigned here to subgenus *Guettardella*, as well as in *A. megacarpa* (Figure 6e). Relatively straight veinlets and regular, rectangular areoles, are well expressed in some Philippine species, e.g., *A. edanoi* (Figure 7e-f), *A. paxillata* (Figure 8a), *A. ramosii*, and *A. tayabensis* (Figure 8c-d). In the Australian taxa, (e.g., *A. tenuifolia*, Figure 8e-f), with the exception of *A. ovatifolia*, the areoles are elongate but quite irregular and the veinlets strongly curved. *Antirhea inconspicua*, from Fiji and Samoa, has areoles that may be elongate or square in the same leaf. In *A. paxillata* (Figure 8a) the minor veins are more or less perpendicular to the secondaries, and the areoles form groups of exactly parallel rectangles in the intersecondary panels—a pattern that seems to culminate a trend toward a distinctly lineolate disposition of minor venation termed "reticuli-paxillate" by Melville (1976). Patterns of minor venation are roughly correlated with leaf blade texture (species with strongly lineolate minor venation tend to have relatively thin blades), nodal anatomy, and inflorescence dimorphism. Venation thus proves to be useful in delimiting subgenera.

Lineolate venation patterns similar to those observed in *Antirhea* have been reported in such rubiaceous genera as *Bobea* Gaud., *Timonius* DC., *Neolaugeria* Nicolson, *Tammsia* H. Karsten, *Hippotis* Ruiz & Pavon, *Sommera* Schlechtend., and *Habroneuron* Standley, among others (cf. Schumann, 1891; Pray, 1953, 1959; Melville, 1976; Nicolson, 1979; Darwin, 1980), and also in some Ochnaceae (Nicolson, 1979) and Quiinaceae (Foster, 1950, 1952). Foster (1950, 1952) and Pray (1959), from an ontogenetic study of lineolate venation in *Quiina* and *Bobea elatior*, concluded that elongate minor venation is derived from similarly oriented, elongate cells in the plate meristem of the developing leaf. Considering the high degree of variability in venation pattern in species we studied, as well as the fact that most genera of tribe Guettardeae are polymorphic for leaf venation, the "reticuli-paxillate" pattern probably arose several times in Guettardeae (in *Antirhea*, *Bobea*, *Timonius*, and *Neolaugeria*) in parallel fashion.

Domatia—Jacobs (1966) summarized four elemental forms of domatia: a pit in the leaf surface, a tuft of hairs, a dome with an opening in its roof, and a pocket of tissue in a nerve axil. The first three types are found in most *Antirhea* species, and the combinations of a pit with tufted hairs (*A. sphaerocarpa*), or a pocket with a tuft of trichomes (*A. ioensis*) are also present. In addition, dome-type domatia are often minutely pubescent at their openings and inside. Jacobs asserts that domatia occur generally in species occupying humid habitats; among Rubiaceae, they are generally absent in herbaceous taxa. *Antirhea* species from wet forests were found to have domatia, but *A. bifurcata*, *A. buruana*, and *A. inconspicua*, all from dry forests, also possess them. Among species lacking domatia, *A. madagascariensis* and *A. putaminosa* occur mainly in dry habitats, as suggested by field notes.

Among species examined, domatia-type is partly correlated with leaf blade texture and pubescence. For example, dome-type domatia are found on chartace-

Figure 7. Venation patterns in selected species of *Antirhea*. a. *A. attenuata* (*FB 1867*), × 8. b. Same, × 20. c. *A. chinensis* (*Ford* s.n.), × 8. d. Same, × 20. e. *A. edanoi* (*BS 44015*), × 8. f. Same, × 20. g. *A. ioensis* (*McMillan 5048*), × 8. h. Same, × 20.

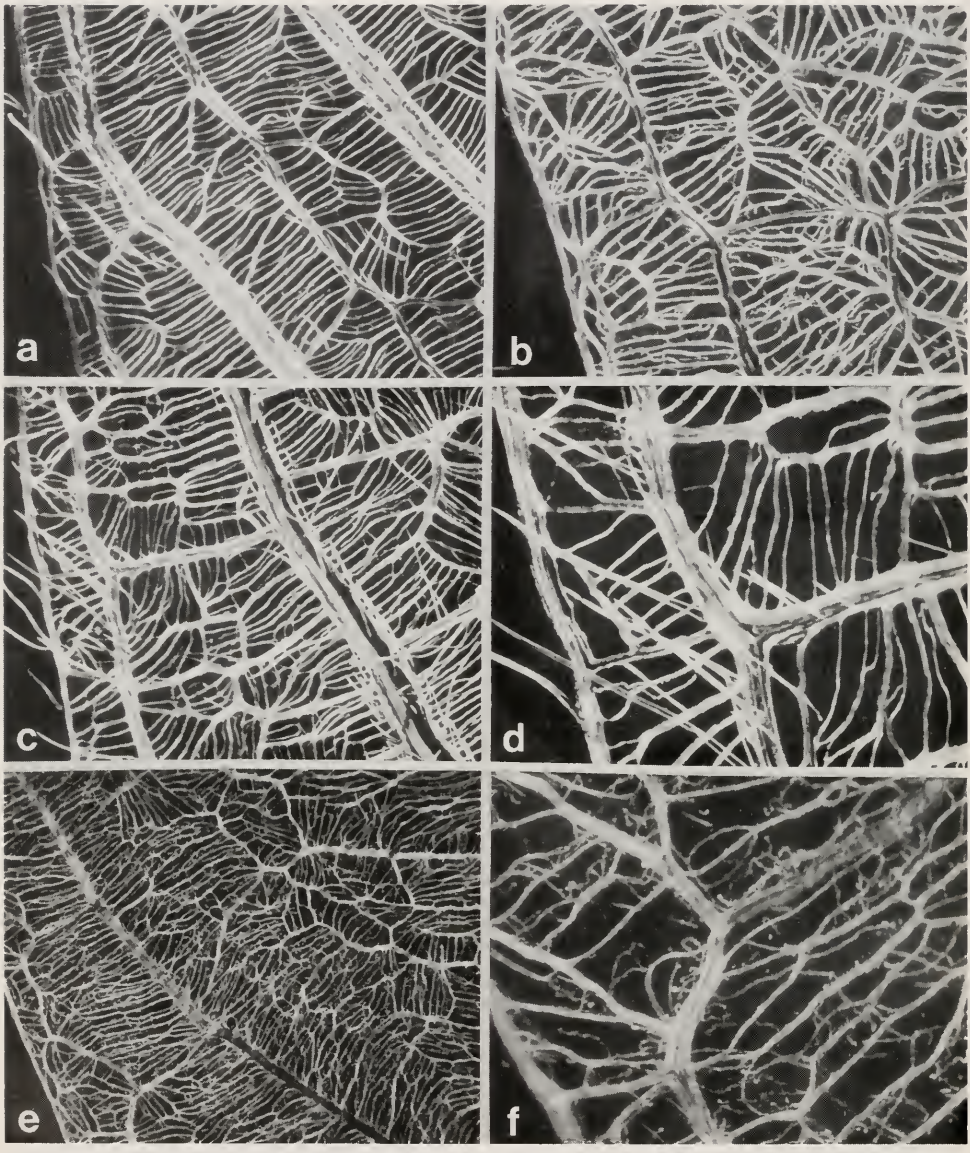


Figure 8. Venation patterns in selected species of *Antirhea*. a. *A. paxillata* (*BS 79440*), × 8. b. *A. rhamnoides* (*Prony 1950*), × 8. c. *A. tayabensis* (*BS 26368*), × 8. d. Same, × 20. e. *A. tenuiflora* (*Brass 182*), × 4. f. Same, × 20.

ous to coriaceous and less densely pubescent leaves (*A. bifurcata*, *A. borbonica*, *A. megacarpa*, *A. smithii*), whereas domatia of tufted hairs predominate on membranaceous to chartaceous (sometimes subcoriaceous) leaves with denser indument. Moreover, domatia of the latter type are often also present in axils of tertiary and higher-order veins (Figure 3d). While the number of domatia per leaf is variable within a taxon, the domatium type appears to be regular in each *Antirhea* species.

Sexual system—As far as we can determine, all species of *Antirhea* are dioecious with dimorphic staminate and pistillate flowers restricted to different plants. In staminate flowers, the epipetalous stamens release abundant pollen, sometimes before the corolla is fully open. In pistillate flowers, the staminodia resemble fertile stamens, but are much smaller and produce no pollen. In staminate flowers, a pistillodium is present, this usually 2-celled and sterile (see discussion for androecium and gynoecium below). We have no reliable or detailed information about pollination biology in the genus, except what can be inferred from specimen notes (see discussion of corolla below). Likewise, our conclusion as to strict dioecism in *Antirhea* is founded entirely upon study of herbarium material and is at present unsupported by field observations.

Inflorescences—Inflorescences (♀ and ♂) are axillary, pedunculate, usually bifurcate cymes, but range from solitary flowers (♀ or rarely ♂ plants) to variously dichotomous (♀ and ♂) or thyrsoid (only in ♂ inflorescences of *A. multiflora*, some *A. hexasperma*, and occasionally *A. inconspicua*). Various orders of branching may be found in the same species.

In species from Indian Ocean islands, staminate and pistillate inflorescences are similar in their dichotomous branching patterns, although the number of flowers is variable within each species. Among the other species, staminate inflorescences are more extensively branched and have more numerous flowers than do pistillate inflorescences, but in both the rachides are usually contracted and the flowers sessile to subsessile and frequently secund.

Since the compound, dichotomous thyrse with flower number roughly the same in staminate and pistillate inflorescences is found throughout tribe Guettardeae, we assume that that structure as well as inflorescence isomorphy are ancestral for *Antirhea*. From such an inflorescence, two different evolutionary trends can be hypothesized. In one scenario, the compound dichasia were retained in both pistillate and staminate plants, but the rachides were suppressed, resulting in a dichotomous inflorescence with usually subsessile and secund flowers. Alternatively, there was a progressive diminution of some or all rachides as well as flower number; if such reduction were more extensive in pistillate than in staminate inflorescences, the result would be the sharp inflorescence dimorphism seen among the majority of our species—as well as species of other Guettardeae (e.g., *Timonius*). This second hypothesis assumes the evolution of inflorescence dimorphism after the establishment of dioecism in the genus. The staminate inflorescence of *A. bombysia*, lacking bracts as well as central flowers, perhaps represents a third, independent instance of reduction in the genus.

Inflorescence bracts—Bracts are usually present near the distal end of the peduncle, are similar in pistillate and staminate inflorescences, and generally resemble the floral bracteoles (discussed below) in shape and size. Occasionally the bracts are quite conspicuous and stipule-like (some ♂ plants of *A. hexasperma*, *A. inconspicua*, and occasionally *A. megacarpa* (*BW 5804*); ♂ and ♀ inflorescences of *A. multiflora*). Because broad bracts are associated with much-branched and many-flowered staminate inflorescences, it seems likely that well-developed inflorescence bracts are primitive in the genus.

Bracteoles are present and persistent beneath flowers in all species examined. Small, vestigial bracteoles are found mainly in the western and eastern geographical range of the genus (subgenera *Antirhea* and *Mesocarpa*, and occasionally in *A. tenuiflora*). In other regions, bracteoles are more conspicuous, particularly in some Philippine species, e.g., *A. benguetensis* and *A. tayabensis*, where they are about the size of calyx lobes (to 9 mm long). In the presumably primitive inflorescences of *Antirhea hexasperma*, *A. inconspicua*, and *A. multiflora*, bracteoles are linear to acicular (about 2.5 × 0.5 mm); from this type of bracteole phyletic reduction and expansion may have taken place. In *A. bombysia* bracteoles are often missing, and we assume this to be the result of extreme reduction within subgenus *Guettardella*. As discussed below, bracts and bracteoles may aid in fruit dispersal.

Calyx—The calyx of *Antirhea* is comprised of four (rarely three) lobes united basally into a short tube, or the calyx may be cupular and irregularly and shallowly lobed to subtruncate (e.g., subgenus *Mesocarpa*). The lobes or segments may be open in bud or slightly imbricate. The opposite pairs of calyx lobes are frequently unequal in size and shape, and this is particularly striking in some Philippine species. The persistent calyces are somewhat enlarged in fruit. The calyx of subgenus *Mesocarpa* is peculiar in being generally coriaceous, nearly globose in bud, and often irregularly ruptured by the expanding corolla.

Corolla—Corollas of *Antirhea* are gamopetalous, actinomorphic, and typically 4-lobed (sometimes 3-lobed in *A. bombysia* and *A. ternata*), or rarely 5-lobed (*A. bifurcata* and *A. chinensis*), and reported as greenish, white, cream-colored, yellow, or sometimes orange-red to dull red. The significance of corolla color is unknown, as we have no information about pollination biology in the genus; the flowers are all apparently odorless. Corollas of staminate flowers are usually salverform, but typically infundibular (often narrowly so) in pistillate flowers. The tubes usually are slender, in staminate flowers 2.5—13 mm long, in pistillate flowers 1—7 mm long, densely to sparsely pubescent without (except at very base), and mostly pubescent (rarely glabrous) toward base within. Corolla lobes are ovate, acute to obtuse at apex, and imbricate in bud (at least one side of each lobe overlapping its neighbor's margin). One of the lobes is entirely exterior, but sometimes one margin is valvate with a neighboring lobe. Hooker (1873) described the corolla of *Antirhea* as having two exterior lobes, but that condition we have observed only in some specimens of *A. smithii*. The occasional 3-lobed corolla is perhaps derived through loss of one lobe.

Androecium—In staminate flowers, the number of stamens generally equals the number of corolla lobes, this being 4, or sometimes 3 or 5. The stamens alternate with the corolla lobes and are attached as much as 1.5 mm below the throat. The anthers are glabrous, sessile to subsessile, their tips exserted. In pistillate flowers, the staminodia resemble stamens in number and position, but are sterile, shorter, and usually well included.

Pollen samples from 21 species were prepared according to Erdtman's (1960) acetolysis method. Microspores of *Antirhea* are uniformly and decidedly semitectate with a reticulate tectum, frequently inaperturate or with one obscure pore,

or rarely 3-porate with unbordered apertures (Figure 1c-d). The grains are spheroidal, (22—) 25—31 (—35) μm in diameter among the specimens examined.

Gynoecium—Ovaries of pistillate flowers are 2- to 12- (16-)celled with one ovule in each cell. The styles are branched, with the number of branches usually the same as the number of cells in the inferior ovary. The style branches are slightly to conspicuously exserted, linear to filiform, and frequently unequal in length. In staminate flowers, the abortive ovary is small or even obscure (to 1.5 mm long) and mostly 2-celled; the style is short relative to that of the pistillate flower and usually bifurcate, the slender branches linear to acicular, included, and often unequal in length.

Pistillate ovaries of subgenus *Mesocarpa* are 8- to 12- (16-)celled, while those of subgenus *Antirhea* are 2- to 3- (4-)celled. Ovaries of subgenus *Guettardella* have an intermediate number of locules (3—11); species of that subgenus with 6 or more locules are confined to the Moluccas (*A. hexasperma*) and New Guinea (*A. multiflora*) and are further characterized by their complex, many-flowered (primitive ?) inflorescences. The number of ovary cells is variable, often within a species. The gynoecium in staminate flowers of *Antirhea talaudensis* is unusual in that the ovary cells and style branches are of the same number and size as in pistillate flowers, although the style is included (due to the longer corolla tube). The unique gynoecium of *Antirhea talaudensis* might thus represent a relict, ancestral condition in the evolution toward dimorphism in staminate versus pistillate gynoecia.

The solitary ovules of *Antirhea* are pendulous and usually laterally compressed toward apex; a slightly thickened apical funiculus is discernible, and the placenta is somewhat swollen above each ovule.

Fruits and seeds—Fruits of *Antirhea* are indehiscent drupes with a 2- to 12- (16-)celled putamen evidently derived from as many united, single-seeded pyrenes. When mature, fruits are crowned by the persistent calyx and subtended by 1—3 bracts or bracteoles (these often lacking in *A. bombysia*). The persistent calyx and bracts are often somewhat enlarged in mature fruits, and the disc also may be expanded (*A. megacarpa*, *A. ovatifolia*, *A. nova-britanniensis*, *A. schmutzii*, *A. smithii*). Fruits range in shape from subglobose, obovoid, or ellipsoid, to rhomboid, and are pubescent to glabrous. The exocarp is reported as red (immature ?) to dark purple or nearly black, the mesocarp as thinly fleshy. The pyrene walls fuse during development to form the stony or ligneous putamen. Drupes with fused pyrenes prevail among Guettardeae (exceptions being the New World genus *Machaonia*, and the Old World genera *Bobea* and *Timonius*), but since the pyrenes are separate early in fruit development (at least in paleotropical *Antirhea* and some *Guettarda* species), fusion may be a derived character state that arose more than once in the tribe.

Fruits of our species fall into two size groups. The larger fruits have a distinct and firm layer of fibrous mesocarp; empty cavities are present in the mesocarp, the number of cavities equalling the number of pyrenes (Figure 12o-p). Such fruits, probably buoyant in seawater, are confined to subgenus *Mesocarpa*, which

includes such widespread species as *Antirhea megacarpa*. The sclerified and chambered mesocarp is likely a derived character, since it is not reported in related genera (i.e., *Timonius* and *Bobea*). Fruits of subgenera *Antirhea* and *Guettardella* are relatively small and lack a well developed mesocarp, but the persistent calyx and bracts are often enlarged. In subgenus *Guettardella* the calyx lobes are reported as green to orange-red, which suggests dispersal by frugivorous birds. Van der Pijl (1969) itemized several plant features associated with bird dispersal, of which the above-mentioned fruits qualify in having an inner protection for the seed against digestion (the putamen), signaling colors when mature, and no smell (field notes report no fruit odor for any *Antirhea* species). In addition, fruit size (less than 15 mm long) supports the assumption that some fruits are bird-dispersed.

The number of seeds per fruit is usually much fewer than the number of ovules, suggesting that rate of pollination or fertilization success is low, or that seed abortion is high. The seeds are consistently narrowly cylindric, sometimes somewhat laterally compressed, and pale brown when dry.

Chromosome numbers—We have found no chromosome counts reported for any of the species here assigned to *Antirhea*, and our own attempts to make counts from pollen mother cells, or from root tips, have been unsuccessful.

Generic Relationships

Antirhea has been placed in Rubiaceae tribe Guettardeae DC. by taxonomists concerned with intergeneric relationships in the family (cf. Bremekamp, 1952; Verdcourt, 1958; Robbrecht, 1988). Among the twelve genera assigned to the tribe by Robbrecht (1988), all have imbricate or valvate corolla lobes, 2- to many-loculed ovaries with a solitary, pendulous ovule in each cell, and fleshy fruits containing several to many 1-seeded pyrenes, or these united into a plurilocular stone. Seed endosperm is little developed and oily. Raphid crystals are absent, but files of rhomboidal crystals are often embedded in the walls of trichome cells. Species of *Ottoschmidtia* and *Dichilanthe* are peculiar in having zygomorphic corollas, and wood anatomy suggests that the latter genus (as well as *Timonius*) are disparate here (ter Welle et al.,1983), but the genera otherwise hang together rather well and almost certainly represent a monophyletic assemblage (Bremekamp 1952, 1966; Prey, 1953; Verdcourt, 1958). The tribe is tropical and widespread, but, interestingly, absent from Africa except for *Guettarda speciosa* L. Bremekamp (1952) elevated Guettardeae to the rank of subfamily, and this taxonomy was followed by subsequent workers (e.g., Verdcourt, 1958) until Robbrecht (1988) expanded Antirheoideae to a concept approaching Schumann's (1897) [supertribe] Guettardinae.

Within Guettardeae, generic circumscription is difficult and, to date, has been based on relatively few characters. *Antirhea*, in our sense, is distinguished primarily on the basis of fused pyrenes, strongly imbricate corolla lobes, and dioecism; each of those characters is found in other Old World Guettardeae (*Guettarda*, *Bobea*, and *Timonius*), although not in combination. Also, none of those characters seems to have satisfactorily discrete states, and no character is very informative in settling evolutionary relationships. Without more reliable

data, especially for New World genera, we were unable to conduct a detailed cladistic analysis. Nevertheless, we venture the following observations:

Habit: Guettardeae are usually trees or shrubs; the climbing habit in *Malanea* (all?), or the hemiepiphytism of some *Timonius* species is derived.

Calyx: The deciduous calyx that uniquely characterizes *Guettarda* is almost certainly a derived character state.

Sexual system: Most genera of Guettardeae have hermaphrodite flowers, and that is probably the ancestral condition for the tribe, with dioecism having evolved (uniquely?) in *Antirhea*, *Timonius*, and *Bobea* (all Old World). However, sexual systems are sometimes difficult to determine from herbarium material, so this hypothesis is tentative. Polygamodioecism in some species of otherwise dioecious genera (e.g., *Timonius polygamus* (Forst.) Robins.) is a secondary reversion toward hermaphroditism.

Corolla aestivation: Most genera of Guettardeae have distinctly imbricate corolla lobes, but in others (*Timonius*) the distinction between imbricate and valvate aestivation is obscure (Valeton, 1909; Darwin, in press). If tribe Vanguerieae is taken as an out-group, then valvate aestivation would have to be considered ancestral for Guettardeae (Robbrecht, 1988). Alternatively, a derived, valvate aestivation would suggest that *Malanea* and *Chomelia* form a monophyletic group.

Pyrene fusion: The degree of fusion is highly variable in Guettardeae and often incomplete. Developmental evidence supports fusion as a derived character state, although reversion to separate pyrenes is easy to imagine. We are presently unable to determine whether the free pyrenes in *Timonius* and *Bobea* represent an ancestral, or a derived condition supporting monophyly.

Ovary locule number: Most genera of Guettardeae show wide variation in number of locules and, thus, potential number of seeds per fruit. We point out a rough correlation between sexual system and locule (seed) number. In *Malanea* and *Chomelia*, the flowers are, apparently, hermaphrodite, and locules number 2, as is usual for Rubiaceae. Among the other genera of Guettardeae, polygamy and dioecism correspond with a higher locule number; in the dioecious genus *Timonius*, pistillate ovaries may form dozens of uniovulate cells. Whether or not the high number of locules represents a genuine instance of pleiomery (evolutionary multiplication of parts) is questionable, as is a functional (adaptive) relationship between locule number and advancing dioecism. The number of ovules may be high in *Timonius* because the pyrenes are separate; in *Antirhea* and other genera with fused stones, dispersibility of the fruit may impose some adaptive limit to seed number.

Interspecific Relationships

All 36 *Antirhea* species were initially coded for 21 informative characters, but substantial character data proved to be missing for some species, particularly for taxa where staminate or pistillate collections were not available for study. Rather than conduct a phylogenetic analysis with a high proportion of missing character states, we deleted species from the analysis if six or more character states were unknown. Character state polarity was established through comparison with other genera of Guettardeae, particularly *Timonius* DC.

TABLE 1. Distribution of character states among Old World *Antirhea* species. 0 = presumed ancestral state, 1 or 2 = presumed derived state(s), ? = missing data, – = ambiguous data (more than 1 state). Numbered characters are: 1. Habit (0 = shrubs or small trees, 1 = trees over 10 m tall). 2. Stipule aestivation (0 = imbricate, 1 = valvate). 3. Stipule persistence (0 = deciduous, 1 = persistent). 4. Leaf arrangement (0 = opposite, 1 = usually or occasionally whorled). 5. Number of leaf traces (0 = 3, 1 = 1). 6. Leaf blade texture (0 = membranaceous to chartaceous, 1 = coriaceous). 7. Crystal sand in leaf blades (0 = absent, 1 = usually present). 8. Free-ending veinlets (0 = absent, 1 = usually present). 9. Areole shape (0 = square to polygonal, 1 = elongate). 10. Domatia (0 = tufted hairs, 1 = dome-like, 2 = absent). 11. ♀ and ♂ inflorescences (0 = monomorphic, 1 = dimorphic). 12. Number of flowers in ♀ inflorescence (0 = 3 or more, 1 = 1). 13. Inflorescence indument (0 = pubescent, 1 = glabrous). 14. Inflorescence bracts (0 = narrow and usually more than 1 mm long, 1 = scale-like and less than 1 mm long). 15. Calyx lobes (0 = equal or subequal, 1 = unequal). 16. Calyx lobe length (0 = usually less than 1 mm long, 1 = usually more than 1 mm long). 17. Style indument (0 = pubescent, 1 = glabrous). 18. Number of cells per ovary (0 = usually fewer than 6, 1 = usually 6 or more). 19. Floral disc (0 = not enlarged in fruit, 1 = usually enlarged in fruit). 20. Length of fruit (0 = less than 15 mm, 1 = more than 15 mm). 21. Mesocarp (0 = thin and homogeneous, 1 = thick and cavernous).

	Characters																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. *A. bifurcata*	0	1	0	0	0	0	1	0	0	1	0	0	0	1	–	0	1	0	0	0	0
2. *A. borbonica*	1	1	0	1	0	1	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0
3. *A. madagascariensis*	0	1	0	1	0	1	1	0	0	2	0	0	1	1	0	0	1	0	0	0	0
5. *A. megacarpa*	1	0	0	0	0	–	0	1	1	1	1	1	0	–	0	0	0	1	1	1	1
8. *A smithii*	1	0	0	0	0	1	0	0	0	1	1	1	–	1	0	0	0	1	1	1	1
10. *A. atropurpurea*	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0
11. *A. attenuata*	?	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
12. *A. benguetensis*	0	–	1	0	1	0	0	1	1	0	1	0	0	0	0	1	–	–	0	0	0
15. *A. caudata*	0	0	0	0	1	0	0	1	1	–	1	1	0	0	0	1	0	0	0	0	0
16. *A. chinensis*	0	1	0	0	1	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0
17. *A. edanoi*	?	–	0	0	1	0	0	1	1	0	?	0	0	0	1	1	0	0	0	0	0
19. *A. hexasperma*	0	–	0	0	1	0	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0
21. *A. inconspicua*	0	–	0	–	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0
22. *A. ioensis*	0	1	0	0	1	0	0	1	0	0	1	1	0	0	–	0	0	0	0	0	0
23. *A. livida*	0	0	0	0	1	0	0	1	–	0	1	1	0	0	–	1	1	0	0	0	0
24. *A. microphylla*	0	–	1	1	1	0	0	1	1	2	1	1	0	0	–	–	1	–	0	0	0
25. *A. multiflora*	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0
26. *A. ovatifolia*	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0
30. *A. ramosii*	?	0	0	0	1	0	0	1	1	0	?	0	0	0	1	0	1	0	0	0	0
31. *A. rhamnoides*	0	1	0	0	1	0	0	1	1	0	1	1	0	0	0	0	–	0	0	0	0
33. *A. talaudensis*	0	1	0	1	1	0	0	1	1	0	1	1	0	0	0	0	–	0	0	0	0
34. *A. tayabensis*	?	0	0	0	1	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0	0
35. *A. tenuiflora*	1	1	0	0	1	0	0	–	1	0	1	0	0	1	0	?	–	0	0	0	0

TABLE 2. Weights assigned to characters in Table 1 after successive (recursive) weighting (Hennig86 *xsteps w* option), and steps per character after construction of Nelson consensus tree based on weighted characters.

	Characters																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Weight	1	2	10	1	10	2	10	3	1	3	1	1	10	3	0	10	1	3	2	10	10
Steps	3	3	1	3	1	2	1	2	4	4	3	4	1	2	5	1	6	2	2	1	1

The resulting data set (Table 1) of 23 species and 21 characters, when analyzed using the Hennig86 program (with the extended branch-swapping option), yielded more than 100 equally parsimonious trees. The Nelson consensus tree generated from the first 100 most parsimonious trees was largely unresolved. Consequently, a system of recursive weighting (Hennig86 *xsteps w* option) was employed. In this procedure, weights are assigned to characters on a 0—10 scale depending on character compatibility (product of character consistency and character retention indices). Final assigned character weights are given in Table 2. The weighted data set yielded three equally parsimonious trees (CI = 71); the Nelson consensus tree (CI = 70) and distribution of character states is shown in Figure 9.

Since we did not include all species of *Antirhea* in the analysis, only limited conclusions can be drawn from the consensus tree (Figure 9). However, the analysis does show three monophyletic species groups, which we recognize as subgenera. Species 1, 2, and 3 (subgenus *Antirhea*) form a monophyletic group supported by the presence of crystal sand in leaf tissues (character 7); other shared (not uniquely) features include valvate stipules, and glabrous styles. The three species are all indigenous to islands of the western Indian Ocean.

Species 5 and 8 comprise a distinctive clade (subgenus *Mesocarpa*) with relatively large (character 20), thick-walled fruits with prominent mesocarp cavities (character 21); they and other species placed in the subgenus also share an arborescent habit, heteromorphic inflorescences, usually many-celled ovaries, and a floral disc that enlarges in fruit. Taxa placed in subgenus *Mesocarpa* extend from the Moluccas and Lesser Sunda Islands to Fiji.

The remaining 18 species included in the analysis comprise a monophyletic group having 1-trace nodes (character 5), as well as free-ending veinlets (as in subgenus *Mesocarpa*), and heteromorphic inflorescences. We place them and 10 other species in subgenus *Guettardella*. Our analysis generally fails to resolve phylogenetic relationships within the subgenus, where many characters show reversals, and most synapomorphies (such as solitary ♀ inflorescences and valvate stipules) are also found in the other subgenera. However, some species juxtapositions are of interest.

The two New Caledonian species (22 and 31) are in close proximity near the base of the *Guettardella* clade. Species 19, from the Celebes, is shown as most closely related to species 25 from New Guinea. Species 10, from the Malay Peninsula, shares a clade with a group of Philippine species (34, 23, and 15). The two Australian species (26 and 35) do not appear to be closely related, and relationships of the Chinese species (16) are ambiguous. While all of the Philip-

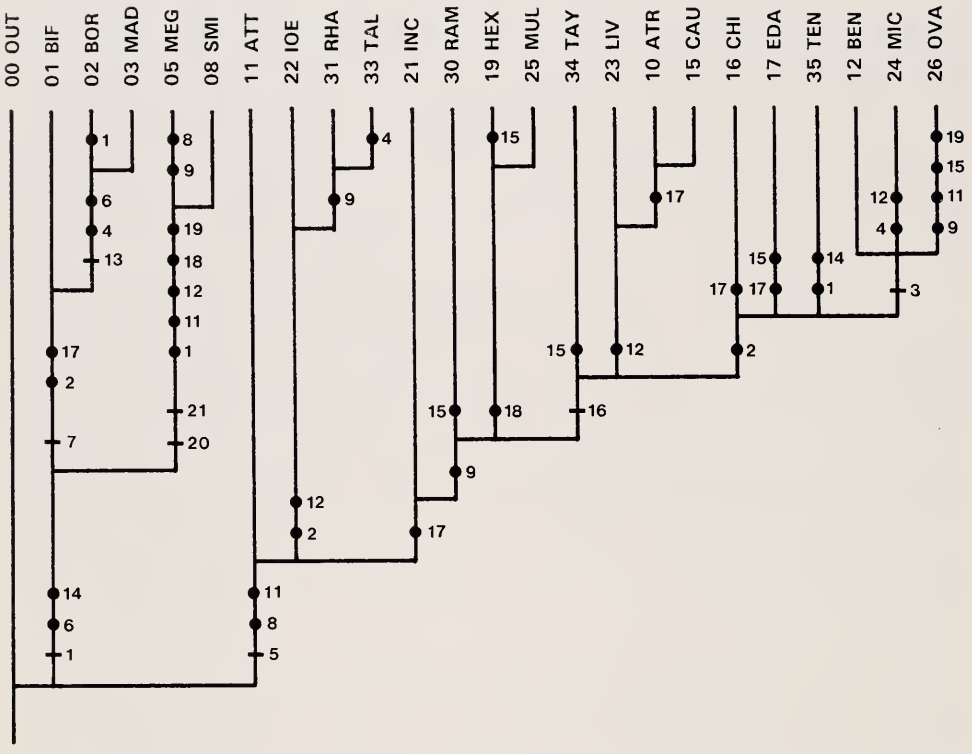


Figure 9. Nelson consensus cladogram showing phylogenetic relationships among selected species of *Antirhea*, based on characters presented in Table 2, with character weights given in Table 3; bar = unique character state change; dot = non-unique character state change or reversal (homoplasy).

pine species of *Antirhea* are members of subgenus *Guettardella*, they do not form a monophyletic group within that subgenus, but instead appear to be allied with species occupying various adjacent land areas.

Taxonomy

The following descriptions, keys, and notes are based on roughly 6200 specimens from thirty herbaria (see acknowledgments for list of institutions). All original descriptions of Old World *Antirhea* species were consulted and, as far as possible, type collections were examined. Lectotypifications are proposed only when we were able to study pertinent herbarium material; pistillate collections, having a greater array of diagnostic features, were preferred as lectotypes over staminate collections. Descriptive terminology follows the outline of characters presented above. Measurements of vegetative parts and fruits were taken from dried material, floral parts were rehydrated for dissection. Field notes and vernacular names are given as they appear on specimens, except where we convert elevations and other measurements to metric units. Collection citations are grouped geographically by country, island, state, province, etc., and then arranged in a sequence from north to south and from west to east. Place names are given as they appear on specimens, except where we correct obvious spelling errors.

ANTIRHEA Comm. ex Juss. Gen. Pl. 204. 1789, Gen. Pl. ed. 2. 226. 1791; Schreber Gen. Pl. ed. 8. 2: 789 (as *Antirrhea*). 1791; Desr. in Lam. Encycl. 3: 688 (as *Antirrhea*). 1792; Comm. ex Juss. in Mém. Mus. Hist. Nat. Paris 6: 377. 1820; Bartling, Ord. Nat. Pl. 212 (as *Antirrhae*). 1830; DC. Prodr. 4: 459 (as *Antirhoea*). 1830; Endl. Gen. Pl. 541 (as *Antirhoea*). 1838; Endl. Ench. Bot. 272 (as *Antirrhoea*). 1841; Lindl. Veg. Kingd. 764 (as *Antirrhoea*). 1846; Walp. Ann. Bot. Syst. 2: 764 (as *Antirhoea*). 1852; Benth. Fl. Austral. 3: 418 (as *Antirrhaea*). 1867; Hook. f. in Benth. & Hook. f. Gen. Pl. 2: 21, 100 (as *Antirrhoea*). 1873; Baker, Fl. Maurit. 144 (as *Antirrhoea*). 1877; Fern.-Vill. Nov. App. 109 (as *Anthirrhoea*). 1880; K. Schum. in Engler & Prantl, Nat. Pflanzenfam. IV. 4: 96 (as *Antirrhoea*). 1891; Boerl. Handl. Fl. Ned. Ind. 2: 79 (as *Antirrhoea*). 1891; Cordem. Fl. Réunion 514 (as *Antirrhaea*). 1895; F. M. Bailey, Queensl. Fl. 759 (as *Antirrhaea*). 1900; Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 7 (as *Antirrhoea*). 1909; Merr. & Perry in J. Arnold Arbor. 26: 233. 1945; Darwin in Allertonia 2: 8. 1979; Jansen in Blumea 29: 565, 568. 1984; Wong in Kew Bull. 43: 493. 1988; A. C. Sm. & S. Darwin in A. C. Sm. Fl. Vit. Nov. 4: 151. 1988. TYPE: *A. borbonica* J. F. Gmelin.

Malanea sensu A. Rich. Mém. Rubiac. 122 (*pro parte*). 1830; non Aublet.

? *Neuropora* Comm. ex Endl. Gen. Pl. 541. 1838, Ench. Bot. 272. 1841; Lindl. Veg. Kingd. 764. 1846; pro syn.

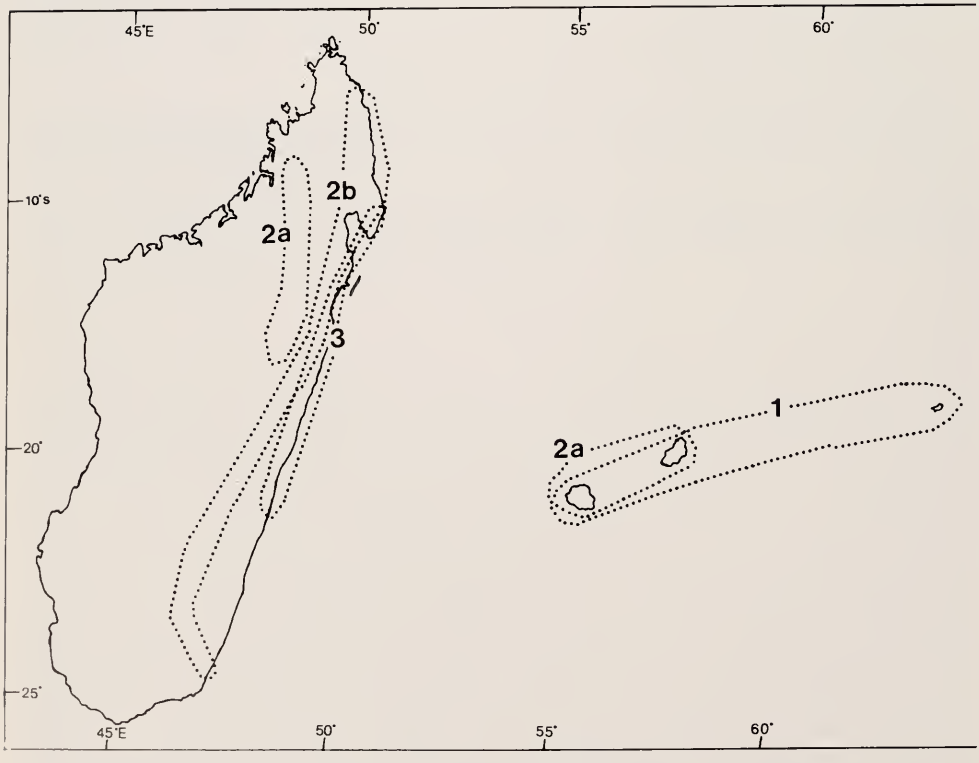
Guettardella Champ. ex Benth. in Hooker's J. Bot. Kew Gard. Misc. 4: 197. 1852; Benth. Fl. Hongk. 158. 1861, Fl. Austral. 3: 418. 1867; Jansen in Blumea 29: 571. 1984. TYPE: *Guettardella chinensis* Champ. ex Benth.

Guettarda sensu Baill. Hist. Pl. 7: 423 (*pro parte*). 1880; non L.

Shrubs to tall trees with stipulate, petiolate, whorled or opposite leaves, the stipules usually sericeous inside and with scattered colleters; leaf blades membranaceous to coriaceous, often dark green above, paler beneath, drying blackish, gradually to abruptly acuminate at apex (rarely retuse and mucronulate), at base often acute to rounded or rarely cordate or attenuate and decurrent onto petiole, the costa conspicuous, canaliculate to plane or sometimes prominulous above, prominent and semiterete beneath, the secondary veins 3—12 on each side of costa, the tertiary veins immersed to prominulous beneath, the areoles usually rectangular or sometimes square, free-ending veinlets rarely present; domatia often present and of variable form; inflorescences axillary, usually spreading, fundamentally dichasial, the flowers usually fewer in pistillate than in staminate inflorescences, or sometimes of roughly the same number in both, the flowers often sessile and secund on inflorescence arms, the inflorescence bracts and bracteoles conspicuous or obscure, persistent; peduncles slender, usually pubescent; calyx tube short, 3- or 4- (5-)lobed, pubescent outside, inside glabrous or pubescent basally; corolla of staminate flowers salverform, the limb spreading, usually 3- or 4-lobed, the lobes imbricate in bud; stamens 3—4 (—5), attached at corolla throat and alternate with lobes, the anthers sessile to subsessile, linear, slightly exserted, dehiscing longitudinally; abortive ovary small, usually 2-celled, the disc minute, puberulent to glabrous, the style cylindric, bifid at apex, the slender branches linear to filiform, included, often unequal in length; corolla of pistillate flowers infundibular and generally similar to corolla of staminate flowers; sterile anthers (staminodia) usually smaller than fertile anthers of stami-

nate flowers; ovary oblong to obovoid, sericeous, 2- to 12- (16-)celled and the style with as many linear, subexserted branches; fruit a drupe surmounted by persistent calyx and subtended by 1—2 persistent bracts, the exocarp thinly fleshy, the mesocarp present or essentially absent; pyrenes 2—12 (—16), united into a bony or woody putamen; seeds cylindric, sometimes somewhat laterally compressed, acute at apex, pale brown when dry.

We recognize 36 species of *Antirhea*, twelve of which are described as new. Geographical distribution of the genus is shown in Maps 1 and 2. Most species are endemic to particular islands, island groups, or limited continental areas, but *A. megacarpa* and *A. tenuiflora* are more widely distributed. Van Balgooy (1971) ascribed *Antirhea* to the New Hebrides, and Jansen (1984) considered Guillaumin's (1932) *Guettarda kajewskii* from that archipelago likewise assignable to *Guettardella*. However, in view of inadequate specimens from the New Hebrides, we refrain from definitely assigning those taxa to *Antirhea*. Roughly 70 percent of the Old World *Antirhea* species occur in Takhtajan's (1969) Indo-Malesian or Good's (1974) Indo-Malaysian Subkingdom (van Balgooy's geographical units IV-VII). About a third of the species are endemic to the Philippines, and we believed that additional species remain to be described from that archipelago.



Map 1. Geographical distribution of *Antirhea* subgenus *Antirhea*. 1. *A. bifurcata*. 2a. *A. borbonica* var. *borbonica*. 2b. *A. borbonica* var. *duplidivisa*. 3. *A. madagascariensis*.

Map 2. Geographical distribution of *Antirhea* subgenera *Guettardella* (dashed line) and *Mesocarpa* (dotted line).

Supported by our phylogenetic analysis (discussed above), we group the Old World *Antirhea* species into three supraspecific taxa, which we recognize here as subgenera. These groups are distinguished on the basis of characters given in the following key.

KEY TO SUBGENERA

1. Crystals forming circular to elongate punctations over abaxial leaf venation; areoles usually square or polygonal; ♀ and ♂ inflorescences similar in branching pattern and number of flowers; inflorescence bracts small and scale-like; fruits small (less than 15 mm long); Madagascar and Mascarene Islands. ..... I. *Antirhea* subgenus *Antirhea* (p. 50)
1. Crystals not evident in leaf blades; areoles mostly rectangular, rarely square; ♀ inflorescences with fewer flowers than ♂ inflorescences; flower bracts distinctly oblanceolate to linear, bristle-like, or deltoid, sometimes scale-like or rarely absent; fruits small or large (more than 15 mm long); southeastern Asia, Malesia, New Guinea, Australia, and Pacific.
   2. Vascular traces 3—4 in leaf scars; leaf blades mostly coriaceous, glabrous above except near base of costa; inflorescence bracteoles deltoid to scale-like; fruits large, (15—) 20—45 mm long, the mesocarp well developed, sclerified, and with the same number of cavities as fused pyrenes. ..... II. *Antirhea* subgenus *Mesocarpa* (p. 59)
   2. Vascular trace 1 in each leaf scar; leaf blades mostly chartaceous to membranaceous, sometimes coriaceous, usually sparsely puberulent adaxially or glabrous; inflorescence bracteoles oblanceolate to linear or bristle-like, rarely deltoid or absent; fruits small, less than 15 mm long, the mesocarp thin or essentially absent. . III. *Antirhea* subgenus *Guettardella* (p. 69)

I. **ANTIRHEA** subgenus **ANTIRHEA**

TYPE: *Antirhea borbonica* J. F. Gmelin.

Trees to 25 m tall, or sometimes shrubs; branchlets 1.5—4 mm broad toward apex; stipules valvate; petioles with 3 vascular traces toward base; leaf blades chartaceous to coriaceous, the secondary veins 2—6 on each side of costa, undersurfaces with circular to elongate clusters of crystals visible over venation; domatia present in axils of secondary veins, dome-like, sometimes absent; staminate and pistillate inflorescences similar in branching pattern (once- to twice-dichotomous) and flower number, the inflorescence arms frequently reflexed; bracts small, deltoid to small and scale-like; calyx tube short, 4-lobed, the lobes small, deltoid; fruits ellipsoid to subglobose, ribbed or not, the exocarp thinly fleshy, the mesocarp mostly absent; pyrenes 2—3 (—4).

Antirhea subgenus *Antirhea* is a monophyletic group of three species endemic to Madagascar and the Mascarene Islands. All species of the subgenus have conspicuous crystal-containing cells distributed over the abaxial leaf venation; other unifying characters are given in the above key. Subgenus *Antirhea* appears to be most closely related to subgenus *Mesocarpa*, which also includes tall forest trees.

KEY TO SPECIES OF *ANTIRHEA* SUBGENUS *ANTIRHEA*

1. Leaves 2 at each node, usually chartaceous to subcoriaeous; style branches 3 in ♀ flowers; fruits subglobose, 3-sulcate; seeds or putamen locules 3; Mascarene Islands. ..... 1. *A. bifurcata*
1. Leaves 3 (rarely 2) at each node, coriaceous; style branches 2 (rarely 3) in ♀ flower; fruits ellipsoid to ovate-ellipsoid; seeds or putamen locules 2, occasionally 3.
   2. Leaves sparsely puberulent to nearly glabrous on both surfaces; secondary veins 4—6 on each side of costa; domatia present on lower leaf surfaces; inflorescences (♂ and ♀) with (5—) 20—100 (—150) flowers; Mascarene Islands and Madagascar. ..... 2. *A. borbonica*

2. Leaves glabrous on both surfaces; secondary veins 2—3 (—4) on each side of costa; domatia absent; inflorescences with 3—7 flowers; Madagascar. ..... 3. *A. madagascariensis*

1. **Antirhea bifurcata** (Desr.) Hook. f. in Benth. & Hook. f. Gen. Pl. 2: 100 (as *Antirrhoea*). 1873; Verdc. in Kew Bull. 37: 571. 1983; Jansen in Blumea 29: 569, *fig. 2*. 1984. FIGURES 6a, 10a-f

Malanea bifurcata Desr. in Lam. Encycl. 3: 688. 13 Feb. 1792; DC. Prodr. 4: 460. 1830.

Tournefortia bifida Lam. Tabl. Encycl. 1: 417. 30 July 1792; Poiret in Lam. Encycl. 5: 360. 1804, in Cuvier, Dict. Sci. Nat. 41: 177. 1826; J. E. Smith in Rees, Cycl. 36: sub sp. no. 25. 1817; Baker, Fl. Maurit. 202. 1877; non *T. bifida* Bojer, Hortus Maurit. 234. 1837 (*nom. illeg.* = *T. bojerii* A. DC. Prodr. 9: 516. 1845, Boraginaceae).

Antirhoea frangulacea DC. Prodr. 4: 460. 1830; Bojer, Hortus Maurit. 168. 1837; Baker, Fl. Maurit. 144 (as *Antirrhoea*). 1877; I. B. Balf. in Philos. Trans. 168: 347 (as *Antirrhoea*). 1879; Tirven. in Maurit. Inst. Bull. 9: 15 (as *Antirhea*). 1980.

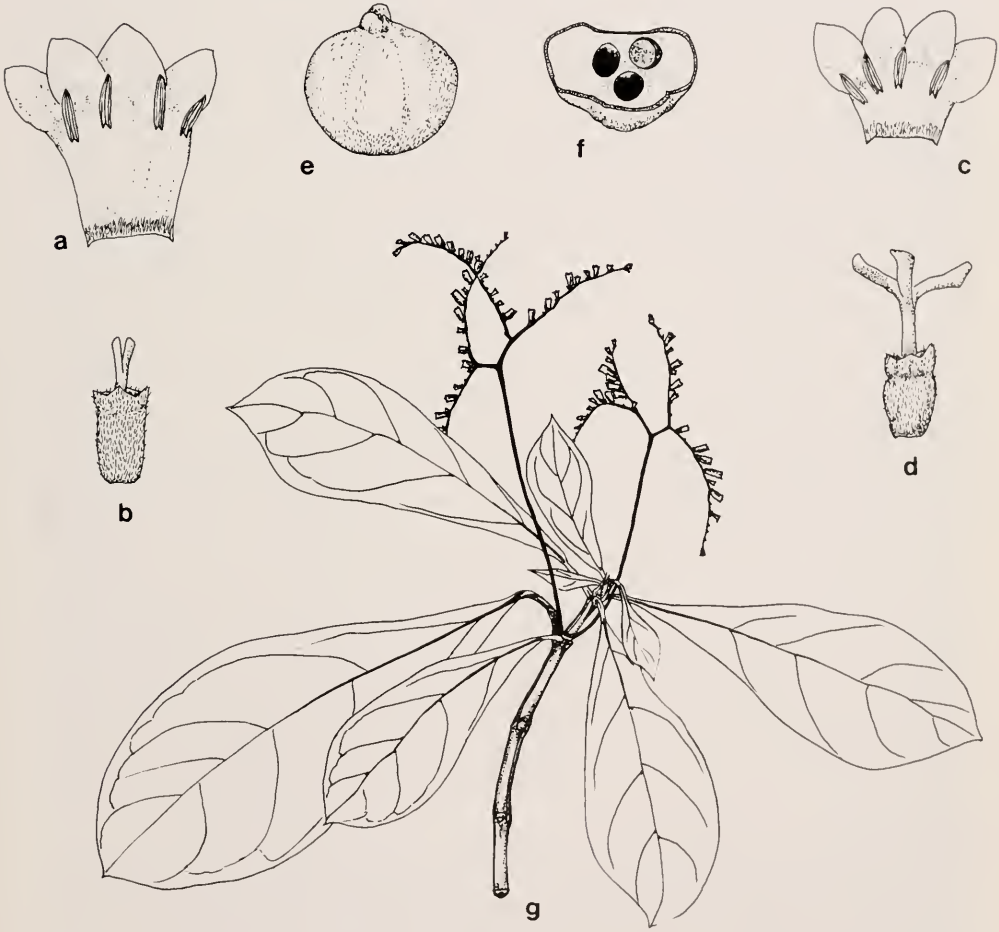


Figure 10. a—f, *Antirhea bifurcata* (a–b from *Sieber maurit. exc. 2. n. 59.* ♂; c–d from *Sieber maurit. II. 199* ♀; e–f from *Blackburn* s.n. ♀). a–b. ♂ flower, × 5. c-d. ♀ flower, × 5. e. Fruit, × 5. f. Cross section of fruit, × 5. g. *A. borbonica* var. *duplidivisa* (*27778-SF (Capuron)* ♀), habit showing twice dichotomous inflorescence (after anthesis), × 0.5.

Guettarda frangulacea Sieber ex DC. Prodr. 4: 460, pro syn. 1830; D. Dietr. Syn. Pl. 1: 788. 1839.
Stenostomum? bifurcatum (Desr.) DC. Prodr. 4: 460. 1830; non *S. bifurcatum* Griseb. Fl. Brit. W. Ind. 333. 1861.
Antirhea bifida (Lam.) Johnston in J. Arnold Arbor. 16: 166. 1935.

Shrub or small tree to 3.5 m tall; branchlets ca. 1.5 mm broad toward apex, compressed and glossy-puberulent, becoming terete and glabrous except above leaf and stipule scars, yellowish to dark brown, the lenticels pale, inconspicuous; stipules valvate, coriaceous, lanceolate, 2.8—5 × 1.5 mm, acuminate, puberulent outside, inside densely sericeous and with scattered colleters; petioles slender, compressed-semiterete and winged, 0.8—1.5 (—2) cm long, to 1 mm broad, sparsely puberulent; leaf blades (broadly) elliptic, chartaceous to subcoriaceous or rarely coriaceous, acute to acuminate at apex, at base acute to cuneate and decurrent onto petiole, (4—) 5—8 (—10) × (2—) 3—5 cm, scattered-puberulent over venation, somewhat more densely puberulent beneath, the costa subplane above, prominulous beneath, the secondary veins prominulous on both surfaces, spreading, 4—6 on each side of costa, the veinlets slightly prominulous beneath, usually forming square areoles, the marginal veins distinct; domatia present in axils of secondary or intersecondary veins, dome-like, the interiors and margins of openings pubescent; ♂ inflorescences dichotomous, the branches often reflexed (occasionally one of them further bifid), (11-) 21- to 35-flowered, at anthesis 2—3 × 2.5—3.5 cm, the flowers secund, subsessile; peduncle slender, 15—25 mm long, to 0.6 mm broad, puberulent; bracts small to obscure, scale-like, broadly deltoid, acute, 0.1—0.3 × 0.2—0.3 mm, pubescent, persistent; calyx tube ca. 0.5 mm high; calyx lobes 4, equal or unequal, usually oblong-deltoid, subcoriaceous, 0.2—0.4 mm long, 0.4—0.6 mm broad at base, acute or obtuse at apex, scattered-puberulent outside, inside pubescent basally or glabrous; corolla salverform, the tube 2.5—4.5 mm long, ca. 0.8 mm diam. at middle, sparsely puberulent to subglabrous outside, inside sericeous near base, the limb 3.5—5 mm broad, the lobes 4, ovate, 1—1.6 × 1—1.5 mm, acute to obtuse, scattered-puberulent outside but scabrous toward margin; stamens 4, inserted ca. 0.5 mm below throat, the anthers sessile, linear, 1.5—2 × ca. 0.3 mm, their tips exserted; abortive ovary to 1.5 mm long, 2-loculed, the style to 1.5 mm long, to 0.2 mm diam., glabrous to scabrous, bifid at apex (occasionally trifid and with one branch vestigial), the branches included, to 0.6 mm long; ♀ inflorescences similar to ♂ in size and flower number; corolla infundibular, the tube 1—1.5 mm long, to 1 mm diam. at middle, sparsely puberulent outside, inside sericeous only near base, the limb 3—4 mm broad, the lobes 4 (—5), ovate, 0.8—1.4 × 0.6—1.2 mm, acute, somewhat irregular at margin; staminodia 4 (—5), inserted ca. 1 mm below throat, the anthers sessile, linear, ca. 1 × 0.3 mm; ovary to 1.5 mm long, 0.5—1 mm diam., pubescent, (2-) 3- (4-)loculed, the disc ca. 0.15 mm high, glabrous, the style compressed, to 2 mm long, ca. 0.8 mm diam., glabrous, 2- to 3- (4-)branched at apex, the slender branches to 1.2 mm long, compressed, exserted; fruits minutely puberulent, subglobose, commonly 3-sulcate, 2—3 mm long, 1.5—3 mm diam., crowned by persistent calyx; pyrenes 2—3 (—4); seeds cylindric, brown, acute, 1.5—2 × ca. 0.3 mm.

TYPIFICATION: *Antirhea bifurcata* was based on *Malanea bifurcata*, the type of which is a specimen without definite locality, sent to Lamarck by Dupuy and presumed (erroneously) by Desrousseaux to have originated from the Antilles. We have seen a photograph of the holotype (*Dupuy* ♀) at P. De Candolle quoted Desrousseaux's reference and made the uncertain combination *Stenostomum? bifurcatum*; Grisebach later erroneously attributed de Candolle's combination to a Jamaican taxon. J. D. Hooker transferred *M. bifurcata* to *Antirhea*, although he likewise thought it an American species. *Tournefortia bifida* is typified by a Commerson specimen (♂, P holotype, n.v.; isotype at G!), collected from Mauritius ("Ile de France"). *Antirhea* ("*Antirhoea*") *frangulacea* was based on *Guettarda frangulacea*; the latter binomial appears on the collection *Sieber, fl. maurit. exc. 2. n. 59*, but was never published by the collector, and de Candolle listed the combination only as a synonym. Sieber's collection is composed of both staminate and pistillate specimens. We designate a pistillate specimen at G(!) as the lectotype (isolectotypes at E!, G!, MEL!, MO!, NY!, PRC!, W!); the staminate or sterile specimens (at E!, GOET!, MEL!, PRC!, W!, WU!) are syntypes.

DISTRIBUTION: Mascarene Islands.

ECOLOGY AND FIELD NOTES: Most of the collections seen do not carry field notes. A few are said to have been gathered in semideciduous dry forests and arid uplands at about 200 m altitude; Balfour (cited above) found it "growing on the coralline limestone" at the southwest end of Rodriguez Island. Flowering and fruiting specimens have been collected in March and September, respectively. Ripening fruits are recorded as purple-black.

VERNACULAR NAME: "Bois goudron" (*A. frangulacea* of Balfour, 1879, cited above).

ADDITIONAL COLLECTIONS: **Mascarene Is.** RÉUNION: *Herb. Ventenat* ♂ (G), *Herb. Boissier 376* (p.p.) ♀ (G). MAURITIUS: Yemen, *Lorence 1821* ♀ (MO). Mauritius, without further locality: *Ayers* s.n. ♀ (NY), *Blackburn* s.n. ♀ (GH), *Bojer IV. 53* ♀ (W), *Bojer* s.n. ♂ (G), *Boissier Herb.* s.n. ♀ (G), *Neraud* s.n. (p.p.) ♀ (G), *John Stuart Mill Herb.* s.n. (GH); *Sieber, Maurit. II. 199* ♀ (G), *Sieber, fl. mixta. n. 190* ♂ & ♀ (GOET, MEL, NY, PRC). RODRIGUEZ: *I. B. Balfour* s.n. (BM, E, GH), *Lesouef 106* ♂ (G), *Lesouef 108* ♂ (G).

Antirhea bifurcata is closely allied to *A. borbonica* and *A. madagascarensis*, but differs in having opposite rather than whorled leaves as well as small, 3-sulcate and subglobose fruits. Unfortunately, *A. bifurcata* has not been well collected, and locality, ecology, and habit are not recorded in the majority of specimens examined. We have found one or two young fruits occasionally present in what appear to be staminate inflorescences, but whether or not they mature is unknown. In pistillate specimens it is common that more than half of the flowers do not develop fruits.

Three collections from Rodriguez Island (*I. B. Balfour* s.n., *Lesouef 106*, and *Lesouef 108*) have deltoid stipules that are smaller than those found in Réunion and Mauritius plants, and the leaf apices are often especially acute with sharp tips. In addition, Lesouef's collections have relatively fewer flowers in the staminate inflorescence (as many as nine seen); Balfour's specimen is sterile.

2. **Antirhea borbonica** J. F. Gmelin

Shrub or tree to 25 m tall; branchlets stout, 2—4 mm broad toward apex, trigonal and pubescent to glabrous, becoming terete and sparsely puberulent to glabrous except above stipule and leaf scars, gray-yellow to dark brown, the lenticels pale; stipules valvate, deltoid-lanceolate, coriaceous, 2—9 (—12) × 2—4 mm, acuminate at apex, often keeled, puberulent to somewhat hirtellous to glabrous outside, inside densely pale-sericeous and with scattered colleters near center; leaves in whorls of 3; petioles moderate to stout, semiterete and winged by leaf blade, (4—) 10—15 (—28) mm long, 1.5—2 mm broad, dispersed-puberulent or glabrous beneath, pubescent above; leaf blades obovate to oblanceolate or rarely elliptic, coriaceous, (5—) 7—13 (—19) × (2—) 3—6 (—8) cm, rounded (to acute) and abruptly acuminate at apex, at base acute to cuneate and decurrent onto petiole, sparsely puberulent over venation to glabrous and glossy above, beneath sparsely puberulent to nearly glabrous, the costa subplane to prominulous above, raised beneath, the secondary veins plane to prominulous above, elevated beneath, 4—6 on each side of costa, the veinlets immersed and obscure above, subplane beneath and forming square to polygonal areoles, the marginal vein distinct; domatia in axils of secondary veins, slit-like (immature ?) or dome-like, puberulent to nearly glabrous inside and at openings; ♂ inflorescence once or twice dichotomous, (7-) 12- to 65-flowered, at anthesis 2—5 (—9) × 1.5—5 (—7.5) cm, the flowers subsessile and secund; peduncles compressed, 2—10 (—15) cm long, 1—2 mm broad, sparsely puberulent to glabrous; bracts small, narrowly to broadly deltoid, often subpeltate and ear-like, entire or sometimes irregularly lobed at margin, 0.4—0.7 × 0.6—0.8 mm, pubescent to scattered-puberulent, persistent; calyx tube to 2 mm high, pubescent to scattered-puberulent to glabrous outside, inside densely pilose toward base; calyx lobes 4, deltoid, more or less pubescent on margin, 0.3—0.8 mm long, 0.6—1.2 mm broad at base; corolla salverform, the tube 4—8 mm long, ca. 1.5 mm diam. at middle, pubescent to minutely puberulent outside, inside sericeous near base, the limb 3—5 (—6) mm broad, the lobes 4, ovate, 1—1.5 × 0.8—1.5 mm, acute to rounded at apex, puberulent outside, scabrous at margin; stamens 4 or occasionally 5, inserted ca. 1 mm below throat, the anthers subsessile, linear, 2.5—3 × ca. 0.5 mm, their tips subexserted to exserted; abortive ovary oblong to subobovoid, to 1.5 mm long, pubescent to glabrous, the style terete to somewhat compressed, 2.2—3 mm long, 0.2 mm diam., glabrous, bifid at apex or sometimes undivided, included, 0.3—0.6 mm long., the disc to 0.2 mm high, glabrous; ♀ inflorescence similar to ♂ in size and flower number; corolla narrowly infundibular, the tube 2.5—4.5 mm long, ca. 1 mm diam. at middle, puberulent to scattered-pubescent outside, inside sericeous near base, the limb 2.5—4 mm broad, the lobes 4, ovate, ca. 1 × 1 mm, acute to rounded, pubescent outside; staminodia 4, ca. 1.4 × 0.3 mm, included to slightly exserted; ovary to 1.5 mm long, pubescent or glabrous, the disc glabrous, the style slender, 3—4 mm long, 2- (3-)branched near apex, the slender branches ca. 0.7 mm long, compressed, exserted; fruits sparsely pale-puberulent to glabrous, cylindric to ellipsoid, somewhat compressed, acute at each end, 6—10 mm long, to 4 mm diam., crowned by persistent calyx; pyrenes frequently 2, sometimes 3; seeds cylindric, acute and laterally compressed toward apex, 4—9 × 0.1—0.2 mm, brown.

KEY TO VARIETIES OF *ANTIRHEA BORBONICA*

1. Inflorescences usually once dichotomous; penduncles to 3 cm long; branchlets puberulent or sometimes nearly gabrous when young. ..... 2a. var. *borbonica*
1. Inflorescences twice dichotomous; peduncles (4—) 5—10 (—15) cm long; branchlets glabrous when young. ..... 2b. var. *duplidivisa*

2a. **Antirhea borbonica** var. **borbonica** FIGURES 1c, 2f-g, 3c, 4a-d, 6c-d

Antirhea borbonica J. F. Gmelin, Syst. Nat. 1: 244. 1791, Syst. Veg. ed. 2. 1: 244. 1796; Verdc. in Kew Bull. 37: 571. 1983; Jansen in Blumea 29: 568, *fig. 2*. 1984.
Malanea verticillata Desr. in Lam. Encycl. 3: 688. 1792; Lam. Tabl. Encycl. *tab. 66, fig. 1* (sine nom.) 1791, Tabl. Encycl. 283. 1792; Juss. in Mém. Mus. Hist. Nat. Paris 6: 377. 1820.
Cunninghamia verticillata (Desr.) Willd. Sp. Pl. 1: 615. 1797; Spreng. Syst. Veg. 1: 410. 1824.
Dreyblättrige Cunninghamie Willd. Sp. Pl. 1: 615. 1797, pro syn.
Guettarda barbinervis Sieber ex Cham. & Schlechtend. in Linnaea 4: 190. 1829.
Antirhoea verticillata (Desr.) DC. Prodr. 4: 459. 1830.
Antirhoea Lostaeana Comm. ex DC. Prodr. 4: 459. 1830, pro syn.
Antirhoea dioica Bory ex DC. Prodr. 4: 459. 1830; Bojer, Hortus Maurit. 168. 1837.
Antirhoea dioica β *barbinervis* (Sieber ex Cham. & Schlechtend.) DC. Prodr. 4: 460. 1830.
Antirhoea dioica γ *acuminata* DC. Prodr. 4: 460. 1830.
Guettarda acuminata Sieber ex DC. Prodr. 4: 460. 1830, pro syn.
Guettarda Antirhoea D. Dietr. Syn. Pl. 1: 788. 1839, nom. illeg. (= *Malanea verticillata* Desr.).
Antirrhoea verticillata (Desr.) Baker, Fl. Maurit. 144. 1877.
Guettarda dioica (Bory ex DC.) Baill. Hist. Pl. 7: 377. 1880.
Guettarda verticillata (Desr.) Baill. Hist. Pl. 7: 377. 1880; Cordem. Fl. Réunion, 514. 1895.

TYPIFICATION: Gmelin's species was based on de Jussieu's (1791) generic description and is typified by Commerson's collection, gathered from Réunion ("Ile de Bourbon" or "Bourbon"); the holotype (Herb. Juss. 9793) is reported by Verdcourt (1983) as at P. We have seen two photographs of this collection, which includes staminate, fruiting, and sterile branchlets on two sheets; the pistillate material is herewith designated the lectotype. Although a figure of *Malanea verticillata* was published earlier than the binomial *A. borbonica*, it was in 1792 that Desrousseaux provided the former species with a description. *Malanea verticillata* was also based on Commerson collections made in Réunion and Mauritius ("Iles de Bourbon et France"); the syntypes and isosyntypes, reported by Verdcourt as in P-LA and P respectively, were not available for study, but two Commerson collections at G(!) are probably also isosyntypes; one of the Geneva specimens is pistillate, the other staminate. Dietrich's name *Guettarda Antirhea* is based upon *Malanea verticillata* and has the same type. Chamisso and Schlechtendal published *Guettarda barbinervis* based on *Sieber fl. maurit. 1. n. 61* ♂ (HAL holotype ?, n.v.; isotypes at E!, G!, GOET!, K, MEL!, MO!, NY!, P, PRC!, W!). The type of *A. dioica* Bory ex DC. is apparently a staminate Bory specimen at G(!), collected on Mauritius. The type of *Antirhoea dioica* var. *acuminata* DC. is *Sieber fl. maurit. 1. n. 60*, comprising pistillate and staminate material; we herewith designate the pistillate specimens in G(!) as lectotype (isolectotypes at E!, GOET!, K, MEL!, MO!, NY!, P, PRC!, W!).

DISTRIBUTION: Mascarene Islands and interior of north-central Madagascar.

ECOLOGY AND FIELD NOTES: Ranging in habit from shrubs (1 to 2 m) to small or large trees with trunk diameters to 0.4 meters; the slender, fragile branches are directed upward. Most frequently found in montane wet forests, "*Sideroxylon* thicket," "*Pandanus* thicket with *Osmunda, Cyathea borbonica, Bertiera,*

Gaertnera, Helichrysum yuccaefolium," "moist forest," and "*Phillipia-Phylica* heath" at altitudes from 400 to 1800 meters; occasionally in forests from 130 to 200 m elevation. The leaves are recorded as being dark green and shiny on both surfaces, the flowers as white, or creamy, or yellowish white, and the ripe fruits as dark purple. Flowering between April and December and fruiting between June and February.

VERNACULAR NAMES: Mauritius and Réunion: "Bois de losteau," "Bois de lousteau," "Bois d'osteau," "Bois lousteau," "Gros lousteau," or "Lousteau." Madagascar: "Molompagngady."

ADDITIONAL COLLECTIONS: **Madagascar.** Sobamaloto- [or Sahavolo-] Perinet, *3696-SF* ♀ (P), *3824-SF* ♀ (P), *9372-SF* ♀ (P); Anony, Sihanaka, *Jardin Bot. Herb. 2961* ♀ (P); Maevarano, below Ambatoafo, *3008-SF (Capuron)* ♀ (P); Mt. at the north of Mangindrano, *Humbert & Capuron 25367* ♀ (P); Ambatondrazaka, Ampokafo, *12626RN* ♀ (P). Madagascar, without further locality: *Perrier 6915* ♀ (P), *6920* (P), *6921* ♀ (P); *Boivin* s.n. ♀ (P), *Boivin* s.n. (P); *Chapelier* s.n. (P). **Mascarene Is.** RÉUNION: Plane de Cafres, *Schlieben 10879* ♀ (B); St. Philippe, *Bernardi 14501* ♂ (G, Z), Mare Longue, *Bernardi 15048* ♀ (Z); Tremblet Point, *Schlieben 10942* ♂ (B, Z); Grand Brûle, *St. John 26499* ♀ (BISH, G), *26505* ♀ (BISH, G); Brûle de Baril, *Lorence & Cadet 2740* ♀ (MO). Réunion, without further locality: *I. B. Balfour* s.n. (E); *I. B. Balfour* s.n. ♀ (E); *Boissier Herb.* ♀ & ♂ (G); *Delessert* s.n. ♀ (G); *Ventenat Herb.* ♀ (G). MAURITIUS: Rivière du Rampart, *Commerson* s.n. ♂ (G); Curepipe, *Johnston* s.n. ♂ (E); Mare Longue Plateau, *Lorence 2352* ♀ (MO), 2 km south of Mare Longue, *Fosberg 52679* ♂ (US), Nature Reserve, *Schlieben 10786* ♂ (B, Z); Petrin Nature Reserve, *Bernardi 14596* ♂ (G, Z), *Lorence et al. 1867* ♂ (MO), *Puff 800822-1/1* ♂ (NO); Perrier Nature Reserve near Mare aux Vacoas, *Lorence 1847* ♀ (MO, US); near Black River Gorges Lookout Point, on road to Chamarel, *Puff 800823-1/8* ♀ (NO); Plane Champagne, *Puff 800823-1/4* ♂ (NO); Anefute, Kanaka, *Brüx* s.n. ♀ (BO). Mauritius, without further locality: *Ayers* s.n. ♂ & ♀ (NY, GH), *Blackburn* s.n. ♂ & ♀ (NY), *Boissier Herb.* s.n. ♂ (G), *Bojer IV. 54* ♂ (W), *Bojer* s.n. ♀ (G), *Bouton* s.n. ♂ (NY), *LeRoy Herb.* s.n. ♂ (NY), *Bentham Herb.* s.n. ♂ (NY), *Jacquin f. Herb.* s.n. ♂ (W), *Martin* s.n. (G); *Néraud* s.n. (p.p.) ♀ (G); *Perrotet, fl. mauri. n. 128.* ♂ (G, W), *Sieber fl. maurit 1. n. 60* ♂ (G), *Sieber, fl. mixta. n. 209* ♂ (E, GOET, MEL, NY).

Antirhea borbonica var. *borbonica* is highly variable in its vegetative and reproductive morphology, particularly as to the shape, size and indument of leaves, length of corolla tube in pistillate and staminate flowers, as well as the degree of aggregation of leaves, flowers, and fruits. De Candolle differentiated *A. verticillata* from *A. dioica* on the basis of obovate-oblong leaves and hermaphrodite flowers; moreover, he distinguished two subspecific taxa within *A. dioica* on differences in leaf blade indument. With many more collections now available for comparison, the type specimens of *A. verticillata* and *A. dioica* readily fall within the continuum of variation ascribable to *A. borbonica* var. *borbonica*.

In the collections *Bernardi 14501, Schlieben 10492,* and *St. John 26505,* although some inflorescences are twice dichotomous, the peduncles are distinctly shorter than those of var. *duplidivisa,* and the branchlets are pubescent or nearly glabrous, suggesting assignment to the typical variety. Some recent collections (*Lorence 1847, 2352,* and *Lorence et al. 1867*) have relatively few flowers and fruits (from 5 to 12); in this feature they resemble *Antirhea madagascariensis* described below, although the presence of domatia as well as the flowering and fruiting period (October) ally them with the present variety.

2b. **Antirhea borbonica** var. **duplidivisa** Chaw, var. nov. FIGURE 10g

Omnino idem ac varietas typica sed inflorescentiis dupli-dichotomis, peduncli (4—) 5—10 cm longi, et ramulis juvenibus glabris differt.

TYPIFICATION: The type is *27778-SF (Capuron)* ♀ (P! holotype), collected near Cap-Est, S Antalaha, Madagascar, 19-21 April 1967.

DISTRIBUTION: Endemic to the eastern coast of Madagascar.

ECOLOGY AND FIELD NOTES: Trees 8 to 15 m growing in wet forest at ca. 15 m altitude. Flowering and fruiting between the months of April and October.

VERNACULAR NAMES: "Mantalanina," "Mantalany," and "Mantalaninafotsy."

ADDITIONAL COLLECTIONS: **Madagascar.** Between Tsaratanana and Analamanara (between Nosiarina and Antsirabe-North), *27638-SF (Capuron)* ♂ (P); between Androkaroka and Antalaha, *11113-SF* ♀ (P), *14999-SF* ♀ (P); Mt. Beanjada, *8858-SF (Capuron)* ♂ (P); Maroantsetra, Farankaraina, *6153-SF* ♀ (P), *12075-SF* ♀ (P); Maroantsetra, Cotür Forest, *14204-SF* ♀ (P); Ambodiriana, *5898 RN (Rakodoniama)* ♀ (P), *9732 RN (Razanaprarany)* ♀ (P); NW Tampolo to Fénérive, Forest Analatsara, W of Rantolava, *18176-SF (Capuron)* ♀ (P); Fort Corvot, *5158-SF* (P), *6516-SF* ♀ (P).

Antirhea borbonica var. *duplidivisa* differs from the typical variety in its conspicuously twice dichotomous inflorescences with more numerous flowers and longer peduncles, and in the branchlets, which are glabrous when young. As in the typical variety, leaf blade shape and inflorescence indument are quite variable. Based on collections seen, populations in the southern part of the range have somewhat larger, more obovate and wider leaf blades than have those in the north. Furthermore, variety *duplidivisa* seems confined to a relatively lower altitude, compared to the typical variety.

3. **Antirhea madagascariensis** Chaw, sp. nov. FIGURES 6b, 11

Ex affinitate *Antirhea borbonica* Gmelin sed foliis parvioribus omnino glabris, nervis lateralibus untrinque 2—4, domatiarum absentia, et inflorescentiis paucifloribus (3—7 floribus) differt.

Tree; branchlets ca. 1.5 mm broad toward apex, trigonal or occasionally compressed, becoming terete, dark gray-brown, glabrous except tomentose above stipule and leaf scars; stipules valvate, narrowly lanceolate, slightly keeled, sharply acuminate, to 4 × 1.5 mm, outside glabrous to puberulent at apex, inside white-sericeous and with colleters toward base; leaves usually 3 in a whorl or rarely opposite; petioles stout, semiterete, 2—4 mm long, to 1.5 mm broad, glabrous, winged by leaf blade; leaf blades elliptic to obovate, coriaceous, (2.5—) 4—7 (—8) × 2—3 cm, gradually to abruptly acute at apex, usually acute at base or sometimes decurrent onto petiole, glabrous and glossy on both surfaces, the costa prominulous to canaliculate toward apex on both sufaces, the lateral veins hardly distinguishable to occasionally subplane, 2—3 (—4) on each side of costa, the veinlets forming polygonal areoles; domatia absent; ♂ inflorescences 3- to 7-flowered, dichotomous, at anthesis to 1.5 × 1 cm; peduncles slender, to 35 mm long, ca. 0.6 mm broad, glabrous to sparsely puberulent; bracts small, often deltoid, to 0.8 × 0.5 mm, puberulent adaxially, glabrous abaxially; calyx tube ca. 0.8 mm high, scattered-puberulent outside, inside puberulent at base; calyx lobes 4, subequal, deltoid, coriaceous, ca. 0.5 mm long, 1 mm broad at base, puberulent at margin; corolla salverform, the tube to 4.5 mm long, ca. 1.5 mm diam. at middle, outside pubescent, inside sparsely pilose, the limb ca. 3.5 mm broad, the lobes 4, ovate, to 1.5 × 1.3 mm, acute; stamens 4, subsessile, inserted

Figure 11. *Antirhea madagascariensis* (a, g–j from *9197-SF (Capuron)* ♀; b–d from *9750-SF* ♀; e–f from *Geay 7600* ♂). a. habit, × 0.5. b. ♀ inflorescence, × 2.5. c. Style of ♀ flower, × 2.5. d. Longitudinal section of ovary, showing 2 ovules, × 5. e. ♂ flower, × 2.5. f. Style of ♂ flower. g. seed, × 2.5. h. Fruit, × 2.5. i–j. Cross section of fruit showing 2 and 3 seed-locules, × 2.5.

1 mm below throat, the anthers linear, ca. 2 × 0.3 mm, their tips exserted; abortive ovary obovoid, small, the disc ca. 0.2 mm high, glabrous, the style cylindric, to 3 mm long, ca. 0.3 mm diam., glabrous, bifid at apex, the slender branches included, unequal, to 0.4 mm long, scabrous; ♀ inflorescences similar to ♂ but more spreading, 2- to 7-flowered, at anthesis to 1 × 1.5 cm; calyx resembling that of ♂ flowers; corolla narrowly infundibular, to 2.5 mm long, ca. 1 mm diam. at middle, 4-lobed, the lobes pubescent to glabrous at margin outside, inside glabrous, the limb to 2.5 mm broad; staminodia 4, included,

inserted ca. 1 mm below throat, the filaments to 0.4 × 0.2 mm, the anthers 1.2 × 0.3 mm; ovary glabrous, to 1.5 × 1 mm, 2-loculed, the style cylindric, to 3.5 mm long, ca. 0.4 mm broad, glabrous, bifid (probably trifid sometimes), the slender branches to 1 mm long, exserted; fruits ovate-ellipsoid, somewhat compressed to sometimes trigonal, 5—10 mm long, to 3.5 mm diam., glabrous, dark red-brown when dry, crowned by persistent calyx (ca. 0.2 mm high); seeds 2 or sometimes 3, cylindric, acute at apex, pale brown.

TYPIFICATION: The type is *Service des Eaux et Forets de Madagascar 9750-SF* ♀ (P! holotype), collected from Sakaitoloho, Mananjary, Madagascar, 26 February 1954.

DISTRIBUTION: Endemic to Madagascar along the east-central coast, where it has been collected mostly near Mananjary, isolated collections extending northward to Antalaha.

ECOLOGY AND FIELD NOTES: Occurring in coastal or lowland forests on sand. Flowering and fruiting probably from February to July.

VERNACULAR NAMES: "Merambavy," "Pitsikahidambo," and "Hazombary."

ADDITIONAL COLLECTIONS: **Madagascar.** Mananjary, *F. M. Geay 7600* ♂ (P), *8194* ♀ (P); southwest of Paugalane, *9512-SF* ♀ (P); Anahamaitso-Marosangy-Mananjary, *13684-SF* ♀ (P); Temfolo Forest, north of Fenerive, *9197-SF (Capuron)* ♀ (P); between Ambalabe and Ambohitralanana (= Antalaha), *27755-SF (Capuron)* ♀ (P). Madagascar, uncertain locality: "Ambila Forest," *4928-SF* ♂ & ♀ (P).

Antirhea madagascariensis closely resembles *A. borbonica* in the trigonal juvenile branchlets, whorled and coriaceous leaves, and dichotomous inflorescences. However, in the present species the leaves are smaller and completely glabrous, have fewer secondary veins and denser minor venation, lack domatia, and usually have few flowers per inflorescence. Specimens from the northern part of the range have larger inflorescences with more flowers, and wider, typically obovate leaf blades, but in all these characters they intergrade with more typical specimens. The geographical distribution of *A. madagascariensis* overlaps that of *A. borbonica* var. *duplidivisa* in east-central Madagascar, but the latter taxon extends farther north and south from the sympatric region; they differ in their inflorescence branching patterns, among other features.

II. **ANTIRHEA** subgenus **MESOCARPA** Chaw, subg. nov.

Ex affinitate subgen. *Antirheae* Comm. ex Juss. et subgen. *Guettardellae* Champ. ex Benth., ab utroque fructibus plerumque 20—45 mm longis, mesocarpiis scleroideis conspicuis, et cavitatibus mesocarpii numero pyrenarum aequalia distinctus. TYPE: *Antirhea megacarpa* Merrill & Perry.

Trees to 33 m tall; branchlets 2—6 mm broad toward apex; stipules imbricate; petioles with 3 (—4) vascular traces toward base; leaf blades subcoriaceous to coriaceous, the secondary veins 5—12 on each side of costa and without associated crystal-containing cells, the veinlets frequently forming square or sometimes elongate areoles, these arranged in groups; domatia usually in axils of secondary veins, dome-like, sometimes absent; staminate inflorescence a compound

dichasium, 11- to 31-flowered, the flowers sessile, usually congested and secund on inflorescence arms; bracts small, deltoid to scale-like; calyx tube cupular, truncate to undulate or erose, frequently ruptured by expanding corolla, coriaceous or sometimes chartaceous; disc glabrous; fruits solitary, glabrous to sparsely puberulent, oblong-elliptic to ovoid, somewhat laterally compressed or not, 15—45 mm long, to 26 mm diam., the disc usually expanded; fruits relatively large (to 45 mm long), the mesocarp sclerified, somewhat granular and with approximately the same number of cavities as pyrenes; pyrenes (6—) 8—16.

Subgenus *Mesocarpa* includes five species distributed from eastern Malesia (Moluccas and Ceram) eastward to Fiji, but absent from tropical Australia. The subgenus is characterized by relatively large fruits with a well developed mesocarp, this usually sclerified and containing a number of hollow cavities that give the fruit buoyancy (see especially *A. megacarpa*). Except for *A. smithii* and *A. schmutzii*, species of subgenus *Mesocarpa* appear to be restricted to lowland habitats.

KEY TO SPECIES OF *ANTIRHEA* SUBGENUS *MESOCARPA*

1. Petioles 2—5 mm long; leaf blades obovate to elliptic; branchlets ca. 2 mm broad toward apex; Ambon and eastern Ceram. ..... 4. *A. anodon*
1. Petioles usually more than 5 mm long; leaf blades elliptic or rarely obovate; branchlets usually at least 3 mm broad toward apex (ca. 2 mm broad in *A. smithii*).
   2. Secondary nerves 5—7 on each side of costa; fruit cylindrical-ellipsoid, shallowly 6- to 10-ribbed, 15—28 × 9—18 mm; Fiji. ..... 8. *A. smithii*
   2. Secondary nerves 8—12 (5—7 in *A. megacarpa*) on each side of costa; fruit usually not ribbed, (23—) 28—45 × 17—26 mm.
      3. Veinlets forming lineolate groups, the areoles mostly elongate; secondary veins 5—7 (—8) on each side of costa; leaf blades 8.5—19 cm long, wrinkled along venation when dry; New Guinea and Solomon Islands. ..... 5. *A. megacarpa*
      3. Veinlets not in lineolate groups, areoles largely square to polygonal; secondary veins 8—12 on each side of costa; leaf blades 17—27 × 6—11.5 cm, wrinkled or not when dry.
         4. Leaf blades acute to briefly obtuse at base, puberulent beneath, wrinkled along venation when dry; fruits ellipsoid and laterally compressed, ca. 45 × 26 mm, acute at each end; New Britain. ..... 6. *A. nova-britanniensis*
         4. Leaf blades attenuate at base, sparsely puberulent beneath, not wrinkled when dry; fruits oblong-ovoid, not compressed, to 32 × 20 mm, truncate to obtuse at apex and rounded at base; Flores Island. ..... 7. *A. schmutzii*

4. **Antirhea anodon** (Miq.) Chaw, comb. nov.

Polyphragmon anodon Miq. Ann. Mus. Bot. Lugd.-Bat. 4: 242. 1869.
Timonius anodon (Miq.) Boerl. Handl. Fl. Ned. Ind. 133. 1891; Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 38. 1909.

Habit unknown (probably tree); branchlets ca. 2 mm broad toward apex, strongly compressed, minutely puberulent and reddish to silvery, becoming glabrous and gray-brown, the lenticels obscure; stipules slightly imbricate, coriaceous, deltoid, keeled, to 6 × 3 mm, acute to acuminate, reddish brown outside, inside densely silvery sericeous and with colleters scattered over the proximal half; petioles stout, adaxially canaliculate, 2—5 mm long, 1—2 mm broad, puberulent with reddish hairs as on costa and branchlets; leaf blades obovate to elliptic, subcoriaceous, 9—13 (—21) × 4—7 cm, abruptly to gradually acuminate at apex, cuneate to briefly rounded at base, glabrous above except

minutely puberulent at very base on costa, scattered-puberulent beneath (the hairs denser on costa and secondary veins), the costa conspicuously canaliculate above, raised beneath, the secondary veins canaliculate to subplane above, prominulous beneath, 7—8 on each side of costa, the veinlets immersed and hardly distinguishable above, subplane beneath, forming tetragonal to elongate areoles; domatia obscure, of tufted hairs in axils of secondary veins, or absent; ♂ inflorescences compound dichasia, 11- to 21-flowered, at anthesis probably to 3 × 2 cm, the flowers sessile, congested, often secund on inflorescence arms; peduncles compressed, to 20 mm long, ca. 1 mm broad, reddish brown puberulent; bracts small, scale-like, to 1 mm long, minutely puberulent, persistent; calyx tube cupular-globose, coriaceous, to 1.5 mm high, shallowly 4-lobed, frequently ruptured by expanding corolla, minutely scattered-puberulent outside, inside glabrous to puberulent near base, the lobes to 0.5 mm long, to 2 mm broad at base, rounded at apex; corolla (immature) probably salverform, the tube ca. 5 mm long, 1.5 mm diam. at middle, densely pubescent outside, inside sericeous near base, the lobes 4, ovate, ca. 1 × 1 mm, rounded; stamens (immature) 4, inserted 1.5 mm below corolla throat, the anthers subsessile, linear, to 3 × 0.6 mm; abortive ovary ca. 0.5 mm long, minutely puberulent, probably 2-loculed, the disc hardly distinguishable, glabrous, the style acicular, ca. 2.5 mm long, 0.3 mm diam., minutely puberulent near base, bifid at apex, the slender branches included, to 1 mm long, slightly unequal in length; ♀ flowers and fruits not seen.

TYPIFICATION: *Polyphragmon anodon* is typified by *de Vriese & Teysmann* s.n. ♂ (L! lectotype; isolectotypes at A!, L!, U!), from Ambon, the only collection cited by Miquel. Unfortunately, the type provides no data other than general locality and year of collection (1859-60). Of the duplicate specimens at L, we here designate the one with the most ample material as lectotype. Boerlage had transferred the species to *Timonius* without comment.

DISTRIBUTION: Presently known from Ambon and eastern Ceram.

ECOLOGY AND FIELD NOTES: A suite of sterile specimens was gathered in the month of August at an altitude of ca. 60 meters, without further field notes.

ADDITIONAL COLLECTIONS: **Moluccas.** EASTERN CERAM: Kiandarat, *bb. 25829* (L), *bb. 25832* (L), *bb. 25931* (A, L).

The type collection, with imbricate corolla lobes, is readily assignable to *Antirhea*, even though no pistillate specimens have been seen. The staminate inflorescence and vegetative morphology closely resemble *A. megacarpa*, from which the present taxon differs in having obovate to elliptic, smaller, and basally cuneate to briefly rounded leaf blades, rather short petioles, and veinlets that form mostly square areoles. In addition, their geographical ranges are distinct, *A. megacarpa* being widely distributed in the lowlands of New Guinea.

5. **Antirhea megacarpa** Merr. & Perry in J. Arnold Arbor. 26: 234, *fig. 1B*. 1945.
FIGURES 4e-h, 6e

Guettardella megacarpa (Merr. & Perry) Jansen in Blumea 29: 577. 1984.
Guettardella erythrocarpa Jansen in Blumea 29: 574. 1984.
Guettardella oriomonense Jansen in Blumea 29: 582. 1984.

Guettardella pachyphylla Jansen in Blumea 29: 584. 1984.
Guettardella solomonense Jansen in Blumea 29: 586. 1984.

Tree to 30 m tall; branchlets ca. 3—5 mm broad toward apex, pubescent to sparsely puberulent, occasionally glabrous, gray-brown, the hairs red-brown to pale, becoming terete and glabrous except above leaf and stipule scars; lenticels conspicuous; stipules imbricate and usually twisted at apex, coriaceous, lanceolate, gradually acuminate, 5—9 × 2—4 mm, tomentose outside, inside densely sericeous and with scattered colleters; petioles frequently with many horizontal fissures, adaxially canaliculate, (7—) 15—25 mm long, 1.5—2.5 mm broad, puberulent; leaf blades elliptic, subcoriaceous, (8.5—) 11—19 (—22.5) × (3.5—) 5—10 cm, gradually acuminate at apex, acute at base, glabrous above except toward base of costa, sparsely pubescent beneath (the hairs denser and appressed over costa and secondary veins), the costa canaliculate to subplane distally above, raised and semiterete beneath, the secondary veins 5—7 (—8) on each side of costa, canaliculate to subplane above, elevated beneath, the veinlets distinct beneath, mostly forming reticulate groups of parallel, elongate areoles; domatia rarely present in axils of secondary or intersecondary veins, dome-like but the opening large, the interior and opening pubescent; ♂ inflorescences once to thrice dichotomous, the arms often reflexed, 19- to 31-flowered, at anthesis to 2 × 2 cm, the flowers congested, secund and subsessile on arms; peduncle slender, 33—50 mm long, to 2 mm broad, puberulent; bracts small to obscure, deltoid, acute, to 1.5 × 1.5 mm, puberulent, persistent; calyx cupular-globose, subcoriaceous to chartaceous, to 2 mm high, shallowly 4-lobed to truncate, frequently ruptured by expanding corolla, minutely puberulent outside, inside puberulent near base; corolla salverform, the tube to 13 mm long, 1.5—2 mm diam. at middle, appressed-pubescent outside, inside pubescent near base, the limb to 5 mm broad, the lobes 4, ovate, 2 × 2 mm, acute to obtuse, scattered-puberulent outside but scabrous toward margin; stamens 4, inserted ca. 1.5 mm below throat, the anthers sessile, linear, obtuse at base, ca. 5 × 0.8 mm, their tips exserted; abortive ovary to 1 mm long, 2-loculed, the disc ca. 0.2 mm high, glabrous, the style to 5.5 mm long, to 0.3 mm diam., spreading-pubescent, bifid at apex, the slender branches included, slightly unequal in length, to 1 mm long; ♀ flowers solitary; peduncles to 9 mm long, 1.5 mm broad; bracts deltoid, ca. 1.2 × 1.3 mm; calyx cupular, coriaceous, to 1.5 mm long, irregularly 4-lobed to subtruncate, the lobes to 1 mm long, 2—3 mm broad; corolla infundibular, the tube (immature) ca. 5 mm long, to 1.5 mm diam. at middle, pubescent as in ♂ flowers, 4-lobed; staminodia 4, inserted ca. 1.5 mm below corolla throat, the anthers sessile, linear, ca. 3.5 × 0.6 mm; ovary to 3.5 mm long, 4 mm diam., pubescent, 10- (or more-?)loculed, the disc ca. 0.2 mm high, glabrous, the style ca. 6 mm long, ca. 0.3 mm diam., sparsely pubescent toward base, 9- to 13-branched at apex, the slender branches distinctly unequal, to 2.5 mm long; fruits glabrous, ellipsoid and laterally compressed, acute at each end, to 38 mm long, ca. 25 mm diam., crowned by persistent calyx (this to 3 mm long), and also often the much expanded disc; pyrenes 8—16, forming a hard, irregularly ribbed putamen, the mesocarp sclerified, somewhat granular, and with the same number of cavities as pyrenes; seeds pale brown, to 30 × 20 mm.

TYPIFICATION: The type of *Antirhea megacarpa* is *Brass 946* ♀ (A! holotype; isotype at BRI!), collected in Ihu, Vailala River, Gulf District, Papua, 2 December 1926. *Guettardella erythrocarpa* is typified by *BW 4759* (*Versteegh*) ♀ (L holotype, n.v.; isotypes at A!, CANB!), gathered from a forest garden at "Tafelberg" near Manokwari, Volgelkop, West New Guinea, 27 May 1957. *Guettardella oriomonense* is typified by *NGF 10439* (*White & Gray*) ♀ (L holotype, n.v.; isotypes at A!, BRI!, CANB!, SING!), collected from Oriomo River, Western District, Papua, 21 January 1959. *Guettardella pachyphylla* is typified by *NGF 46553* (*Katik*) ♀ (L holotype, n.v.; isotype at BRI!), gathered from Gogol River, Madang District, North East New Guinea, 17 September 1969. The type of *Guettardella solomonense* is *BSIP 17719* (*Mauriasi et al.*) ♀ (L!), collected from eastern Santa Cruz Island, 20 October 1969.

DISTRIBUTION: New Guinea to the Solomon and Santa Cruz Islands.

ECOLOGY AND FIELD NOTES: Common in lowland primary rain forest or old secondary forest, mainly on clay soil; reported at altitudes from sea level to 60 m (occasionally to 240 m) in habitats inundated during the wet season. Reported as trees with trunk diameters to 0.5 m, the boles usually straight (without buttress), to 20 m tall. The outer bark surfaces vary in color from pale gray to black, mostly recorded as smooth, unfissured, or rarely peeling or finely pustular; the inner bark is white to yellow or orange-straw, without exudate; the wood is creamy yellow to dark straw-colored. Staminate inflorescences frequently have pod-like fungal bodies or galls. Corollas vary in color from greenish white (immature ?) to white, creamy yellow, or yellow. Flowering specimens have been collected from August to February, fruiting material between December and August; the mature fruits are reported as red.

VERNACULAR NAMES: Vogelkop, New Guinea: "Mbeb" or "Mbep" (Salawati Is.), "Seboreroko" (Manikiong); "Wobbrijka;" "Bengemoen" (Hattam); "Foko," "Fokko," or "Jôhko" (Manikiong); "Koeloe;" "Soewelen;" "Wiem," "Wien," or "Wim" (Mooi). Geelvink Bay: "Adoriap;" "Kadoipi;" "Poroere" (Biak). West Sepik: "Bumberi" (near Wewak). Madang: "Palapik" (Kaigorin); "Tituarawa" (Rawa); "Tup" (Bembi). Central: "Kemnasini" (Waria).

ADDITIONAL COLLECTIONS: **West New Guinea.** VOGELKOP: Salawati Is., Kaloal, *BW 1393* (CANB), *BW 1444* (L), *BW 1469* (LAE), *BW 4264* (L); Warsamson valley, E of Sorong, *BW 11571* (L), *BW 11685* (BISH), *11678* (BISH), *BW 12465* (L); Warsamson River, 25 km E of Sorong, *BW 2955* (L); ca. 50 km W of Manokwari, Prafi, *BW 398* (L), Wariki, *BW 5804* ♂ (L); ca. 30 km W of Manokwari, *BW 10834* ♀ (L); ca. 25 km W from Manokwari, *BW 10978* (L); Warmare valley, ca. 25 km SW of Manokwari, *BW 15667* (L); valley of the lower Pami River, ca. 5 km N of Manokwari, *BW 4390* ♂ (CANB, L); Beri Creek near Andai, SW of Manokwari *BW 11925* (BISH); Andai near Manokwari, *BW 7256* (L); Forest Reserve "Tafelberg" near Manokwari, *BW 4338* ♀ (A, CANB, SING). GEELVINK BAY: Japen Is.: Soemberbaba, *BW 11144* ♂ (BRI, CANB, L); Seroei, *bb. 30520* (L, SING); Aisaoe, *BW 10528* (L), *BW 10026* (L). DJAJAPURA: Oereb, ca. 200 km W of Hollandia, *BW 9301* ♀ (CANB, L). MIMIKA: Si-era (= Djera), Oeta (= Uta), *Exped. Lundquist 115* (*bb. 32834*) (L), *260* ♀ (L). **North East New Guinea.** WEST SEPIK: SE of Tadji airstrip near Aitape, *NGF 1235* ♀ (BRI, CANB). MADANG: Sapi catchment, Gogol valley, off Road 213, *LAE 63527* ♀ (BISH); Enecil Village near Gogol River, *NGF 46639* ♂ (CANB); S of Gogol River, near Mawan Village, *Hoogland 4921* ♂ (A, CANB); Aupan logging area, *NGF 46642* (A, BISH, BRI, CANB). MOROBE: between Busu and Butibum River, ca. 7 mi. N of Lae, *Hartley 11439* ♂ (A, CANB, LAE). **Papua.** WESTERN: Oriomo River, *NGF 10438* ♀ (A, BRI, CANB, SING). GULF: W bank, junction of Vailala and Lohiki Rivers, *Schodde & Craven 4293* ♀ (CANB). CENTRAL: Kuriva forestry area, near Veimauri River, *LAE 51564* ♂ (A, BISH, CANB); Brown

River, *NGF 13079* ♂ (A, CANB, SING); Mori River, *NGF 41898* ♀ (A, BISH, CANB); Nunumai, ca. 12 km N of Amazon Bay, *Pullen 7659* ♀ (CANB); Kanosia, *Carr 11760* ♂ (A, L). MILNE BAY: Modewa Bay, Modewa, *Brass 28932* ♂ (A, LAE); ca. 0.5 mi. N of Waigani Plantation, *NGF 1302* ♀ (BRI). **Solomon Islands.** CHOISEUL: E side of Oaka River, *BSIP 18140* ♀ (L, SING). SANTA ISBEL: Gehe River, *BSIP 7732* ♀ (K, L).

Antirhea megacarpa is by far the most frequently collected species of the genus in Melanesia, and the most widely distributed Old World *Antirhea* species. Jansen did not contrast *Guettardella erythrocarpa, G. oriomonense, G. pachyphylla*, or *G. solomonense* with *Antirhea megacarpa*. Although many of the available specimens are sterile, or are fruiting only, the vegetative morphology and characters given in field notes adequately justify the inclusive species definition adopted here. In *A. megacarpa,* leaf size and pubescence are variable even in the same collection or among specimens from nearby localities. Pyrene (or locule) number per ovary likewise does not warrant recognition of separate species; even among the type collections cited above, this character is unstable and overlapping: 8—10 in *G. erythrocarpa*, 9—10 in *G. oriomonense*, 9—14 in *G. pachyphylla*, 6—10 in *G. solomonense*, and 10—12 in *A. megacarpa* (sensu stricto). The shape of young fruits is also variable, and apparently much influenced by the late-developing mesocarp.

The wide geographical distribution of *Antirhea megacarpa* is likely due to the buoyancy of its fruits, which have about the same number of mesocarp cavities as putamen locules. This type of fruit is also found in *A. nova-britanniensis, A. schmutzii,* and *A. smithii* (and possibly *A. anodon*), species to which *A. megacarpa* seems most closely allied. Vegetatively, the sterile specimen *NGF 593* (L!), collected from Bougainville Island, closely resembles *Antirhea megacarpa,* particularly in its robust branchlets, deltoid and imbricate stipules, and large leaves, but the leaves are mostly obovate, domatia are present as impressed pits with pubescent openings, and the veinlets are immersed—all features distinctly different from *A. megacarpa* as here defined; a separate taxon may be represented. In its relatively few-flowered inflorescences and vegetative characters of stipules and venation, *Brass 28518* ♂ (A, CANB, LAE), collected from Rossel Island, Papua, seems also distinct from other *A. megacarpa* specimens.

6. **Antirhea nova-britanniensis** (Jansen) Chaw, comb. nov.

Guettardella novo-brittaniense Jansen in Blumea 29: 580. 1984.

Tree to 33 m tall; branchlets 3—6 mm broad toward apex, compressed and tomentose with pale brown hairs, becoming terete and glabrous except above leaf and stipule scars; lenticels obscure; stipules imbricate, coriaceous, deltoid, 7—8 × ca. 4 mm, gradually acuminate, densely appressed-puberulent outside, inside densely sericeous and with scattered colleters near center; petioles stout to moderate, semiterete to subtriangular near base, canaliculate adaxially, 5—15 mm long, ca. 3 mm broad, densely puberulent; leaf blades elliptic, subcoriaceous, 17—27 × 8.5—11.5 cm, gradually or sometimes abruptly acuminate to acute at apex, acute and briefly obtuse at base, glabrous above except near base of costa, scattered-puberulent beneath, the hairs subappressed to spreading and denser over costa and secondary veins, the costa distinctly canaliculate above, elevated beneath, the secondary veins canaliculate above, raised beneath, 9—10 (—12)

on each side of costa, the veinlets immersed and obscure above, subplane beneath and forming mostly square to rarely elongate areoles, these randomly disposed; domatia usually absent or obscure as tufted hairs in axils of secondary veins; ♂ and ♀ flowers not seen; fruiting peduncels compressed, to 30 mm long, 1.5 mm broad, tomentose, surmounted by 2 minute, deltoid bracts ca. 0.5 × 1 mm; fruits solitary, sparsely puberulent to glabrous, ellipsoid, to 45 × 26 mm, crowned by persistent calyx and expanded disc, the mesocarp granular, with obscure to distinct cavities; pyrenes 10, the seeds cylindric, brown, acute, 20 × 1.5 mm.

TYPIFICATION: The type is *NGF 10058* ♀ (L holotype, n.v.; isotypes at A!, CANB!), collected from Eliak Creek bank, southern New Britain Island, Papua New Guinea.

DISTRIBUTION: Known only from New Britain Island.

ECOLOGY AND FIELD NOTES: Available collections were gathered from trees with trunks to 75 cm diameter, growing on rising ground and limestone covered with red soil at 15—33 m elevation. The bark is reported as brown to pale gray-brown, slightly pustular and shedding in irregular small flakes; the wood as pale cream to orange. Fruiting specimens have been collected in March and May; the fruits are red when mature.

VERNACULAR NAME: "Igey."

ADDITIONAL COLLECTION: **Papua New Guinea.** NEW BRITAIN: Puli River, W side, Kandrian, *NGF 27229* ♀ (A, BRI, CANB).

This species is closely related to *Antirhea megacarpa,* from which it differs in having usually larger and abaxially more pubescent leaves with more numerous secondary veins, veinlets more randomly disposed and usually forming square areoles, and larger fruits. The species also resembles *A. schmutzii* in having numerous secondary veins, but the shapes of their leaves and fruits are strikingly dissimilar. The collection *NGF 27229,* cited above, closely resembles the type collection, but with the petioles longer and the leaf bases more acute. A sterile specimen, *NGF 26533* (LAE), also from New Britain, resembles both *Antirhea megacarpa* and the present species, and is not readily assignable to either taxon.

7. **Antirhea schmutzii** (Jansen) Chaw, comb. nov. FIGURES 3b, 6g-h, 12o-p

Guettardella schmutzii Jansen in Blumea 29: 585. 1984.

Tree to 13 m tall; branchlets 3—4 mm broad toward apex, strongly compressed when young, minutely puberulent and gray-yellowish, becoming glabrous except above leaf and stipule scars; lenticels conspicuous; stipules imbricate, subcoriaceous, deltoid, 6.5—9 × 4—5 mm, gradually acuminate and sometimes twisted at apex, tomentose outside, inside densely sericeous and with scattered colleters toward center; petioles semiterete to subtriangular near base, canaliculate adaxially, (9—) 15—25 mm long, 1.5—3 mm broad, densely to sparsely puberulent adaxially, puberulent to glabrous abaxially; leaf blades elliptic, subcoriaceous, 21.5—25 × 6—10.5 cm, gradually acuminate at apex, acuminate to attenuate and decurrent onto petiole at base, glabrous above except near base

Figure 12. a. *Antirhea paxillata* (*BS 79440* ♂), habit, × 0.5. b—c. *A. putaminosa* (*Simmonds* s.n. ♂). b. Abaxial surface of leaf blade showing retuse apex, × 1. c. Fruit with persistent calyx and bract, and portion of peduncle, × 2.5. d—e. *A. rhamnoides* (*Vieillard 683* ♀). d. Fruit with persistent calyx and bract, and portion of peduncle, × 2.5. e. Cross section of fruit, × 2.5. f—g. *A. ioensis* (*McMillan 5048* ♀). f. Fruit with persistent calyx and bracts, and portion of peduncle, × 2.5. g. Cross section

of costa, sparsely puberulent beneath, the costa distinctly canaliculate above, elevated beneath, the secondary veins canaliculate above, raised beneath, 8—9 (—11) on each side of costa, the veinlets immersed and obscure above, subplane beneath, forming mostly square to rarely elongate areoles; domatia (when present) dome-like in axils of secondary veins, the large openings and interiors puberulent; ♂ and ♀ flowers not seen; fruits solitary on compressed and sparsely puberulent pedicels to 25 mm long and 2 mm broad, the fruits glabrous, oblong-ovoid, (23—) 28—32 mm long, 17—20 mm diam., obtuse to truncate at apex, rounded at base, crowned by persistent calyx (to 2 mm long) and expanded disc (to 4 mm high); pyrenes 8; seeds cylindrical, brown, acute, to 26 × 1.5 mm.

TYPIFICATION: The type is *Schmutz 4820* ♀ (L holotype, n.v.; isotype at L!), gathered at Manggarai, Paku, West Flores, Lesser Sunda Islands, March 1981.

DISTRIBUTION: Known only from the type locality.

ECOLOGY AND FIELD NOTES: Recorded from rain forests at altitudes of 400 to 500 meters. Fruiting specimens have been collected in December and March; the fruits are reported as red when mature.

VERNACULAR NAME: "Muku taa."

ADDITIONAL COLLECTION: *Schmutz 4948* ♀ (L!), from the type locality.

Antirhea schmutzii and *A. nova-britanniensis* are similar, both differing from *A. megacarpa* in their larger leaves with more numerous secondary veins, and randomly disposed veinlets that form mostly square areoles. They differ from one another in the shape and pubescence of the leaf blade, the length of the petioles, and the size of the fruit. Among the species of subgenus *Mesocarpa, A. schmutzii* is characterized by acuminate to attenuate leaf bases, and oblong-ovoid fruits that are truncate to obtuse at apex, rounded at base, and not at all laterally compressed.

8. **Antirhea smithii** (Fosberg) Merr. & Perry in J. Arnold Arbor. 26: 233. 1945; Parham, Pl. Fiji Isl. 187 (as *Antirrhoea*). 1964, ed. 2. 264 (as *Antirrhoea*). 1972. A. C. Smith & S. Darwin in A. C. Smith, Fl. Vit. Nov. 4: 153. *fig. 62A-B, 63A*. 1988. FIGURES 5a-c, 6f

Timonius sp. A. C. Smith in Bishop Mus. Bull. 141: 140. 1936; J. W. Parham, Pl. Fiji Isl. 210. 1964, ed. 2. 295. 1972.
Timonius smithii Fosberg in Sargentia 1: 121. 1942, in Bull. Torrey Bot. Club 70: 393. 1943.
Guettardella smithii (Fosberg) Jansen in Blumea 29: 585. 1984.

---

of fruit showing 5 seed-locules, × 2.5. h—i. *A. hexasperma* (*Hort. Bogor. IV E. 50a*). h. Fruit with persistent calyx, × 5. i. Cross section of fruit showing 6 seed-locules, × 5. j—k. *A. livida* (*Elmer 12968* p.p. ♀). j. Fruit with persistent calyx and portion of peduncle, × 2.5. k. Cross section of fruit showing 3 seed-locules, × 2.5. l—m. *A. tenuiflora* (*Brass 19861* ♀) l. Fruit with persistent calyx, × 2.5. m. Cross section of fruit showing 4 seeds, × 2.5. n. *A. inconspicua* (*Vaupel 84* p.p. ♂), portion of inflorescence and peduncle, showing trifid inflorescence and central, stipule-like bract, × 5. o—p. *A. schmutzii* (*Schmutz 4820* ♀). o. Fruit with persistent calyx, showing expanded disc, × 1. p. Cross section of fruit showing 8 seeds, sclerified mesocarp, and cavities, × 1. b = bracts, c = cavity, i = inflorescence, m = mesocarp, pe = peduncle, pu = putamen.

Shrub or tree to 18 m tall; branchlets 2 mm broad toward apex, brown, compressed, puberulent to glabrous, becoming terete and glabrous except above stipule and leaf scars; stipules imbricate, deltoid, acute to acuminate, 2—4 × 2—3 mm, densely puberulent to glabrous outside, densely sericeous inside and with scattered colleters except near apex; petioles semiterete to subterete at base, distally somewhat winged by leaf blade, 5—15 mm long, ca. 2 mm broad, glabrous to puberulent; leaf blades elliptic to broadly elliptic, rarely ovate, 6—12.5 × 3—5.5 cm, acute at both ends, decurrrent onto petiole, subcoriaceous to coriaceous, glabrous above, puberulent (particularly over costa) to glabrous beneath, the costa subplane above, raised beneath, the secondary veins plane above, prominent beneath, 5—7 on each side of costa, the veinlets obscure above, subplane beneath and forming square or polygonal areoles; domatia rarely present in axils of secondary and tertiary veins, dome-like, slightly puberulent inside; ♂ cymes 11- to 21-flowered, once to twice dichotomous, the flowers sessile or nearly so, each subtended by 1—2 small, deltoid to scale-like bracts; peduncles 1.5—2.5 mm long, ca. 1 mm broad, sparsely puberulent to glabrous; calyx tube cupular, truncate to undulate or erose, to 1 mm high, puberulent outside; corolla salverform, the tube to 14 mm long, ca. 1.5 mm diam. at middle, appressed-pubescent outside, glabrous inside, the limb ca. 6 mm broad, the lobes 4, ovate, ca. 2.5 × 2 mm, acute, pubescent outside; stamens 4, the anthers subsessile, linear, to 6.5 × 0.5 mm, their tips exserted; abortive ovary to 1.5 mm long, sparsely pubescent, brownish, the disc ca. 0.2 mm high, glabrous, the style slender, ca. 4 mm long, 0.2 mm diam., scabrous to papillose, bifid at apex, the slender branches to 0.6 mm long, papillose to sparsely puberulent; ♀ flowers not seen; fruits solitary, thinly fleshy, glabrous, cylindric-ellipsoid, irregularly and shallowly 6- to 10-ribbed, rounded to nearly truncate at both ends, somewhat laterally compressed, 15—28 mm long, 9—18 mm broad, crowned by persistent calyx and frequently also the expanded disc; pyrenes 6—11, arranged in 2 nearly parallel rows and forming a putamen; mesocarp sclerified, somewhat granular with about the same number of cavities as pyrenes; seeds pale brown, to 15 × 1.5 mm.

TYPIFICATION: *Timonius smithii* is typified by *A. C. Smith 1347* ♀ (US! holotype; isotypes at GH!, NY!, P!), collected above Maloku, Moala Island, Fiji, 22 March 1934.

DISTRIBUTION: Endemic to Fiji.

ECOLOGY AND FIELD NOTES: Branches are recorded as ascending and bushy at top. Reported habitats are secondary forest, rain forests, thin or dense forests, and dense bush or thickets of ridge-crests, at altitudes from 30 to 550 meters. Staminate specimens have been collected between October and December; the corollas are white to pale yellow, soon falling away. The ripe fruits are red to dull red and have been gathered from March to July.

ADDITIONAL COLLECTIONS: **Fiji.** VITI LEVU: SERUA: Navua River, between Nakavu & Nukusere, *Horne 820* (K). NAMOSI: Nambukavesi Creek, *DA*, 22 April 1962 (*L9568*) ♀ (BISH). NAITASIRI: Tholo-i-suva, *DA*, 4 April 1962 (*L9566*) ♀ (BISH); Princess Road, Koroiveimbau *DA 7574* ♀ (BISH); Suva Pumping Station, *Degener & Ordonez 13760* ♂ (A, NY, US); vicinity of Nasinu, 9 mi. from Suva, *Gillespie 3522* ♂ (A, BISH, US); Central Road, Suva, *MacDaniels 1147* ♀ (BISH). REWA: Mt. Korombamba, *A. C. Smith et al. 11535* ♀ (BISH). OVALAU: hills W of Lovoni Valley, on ridge S of Mt.

Korolevu, *A. C. Smith 7664* ♀ (BISH, GH, NY, US); summit of Mt. Tana Lailai & adjacent ridge, *A. C. Smith 7685* ♀ (BISH, GH, NY, P, US). VANUA LEVU: MBUA: Lower Wainunu River Valley, *A. C. Smith 1724* ♀ (BISH, GH, NY, US). THAKAUNDROVE: above Naingganggi, *DA 15715* ♀ (BISH, BRI); Vunimoli, *DA 15300* ♀ (A, BISH, BRIS, NY); Natewa Bay region, hills W of Korotasere, *A. C. Smith 1930* ♀ (BISH, GH, NY, P, US).

Antirhea smithii is clearly related to *A. megacarpa*, from which it differs in having more slender branchlets, adaxially subplane (rather than canaliculate) petioles, usually smaller leaf blades, fewer-flowered staminate inflorescences, staminate corolla tubes glabrous inside, and longer anthers.

III. **ANTIRHEA** subgenus **GUETTARDELLA** (Champ. ex Benth.) Chaw, comb. nov.

Guettardella Champ. ex Benth. in Hooker's J. Bot. Kew Gard. Misc. 4: 197. 1852; Benth. Fl. Hongk. 158. 1861., Fl. Austral. 3: 418. 1867; Jansen in Blumea 29: 571. 1984. TYPE: *Guettardella chinensis* Champ. ex Benth.

Shrubs or occasionally trees; branchlets less than 2 mm broad toward apex; stipules imbricate or valvate; petioles with 1 vascular trace toward base; leaf blades membranaceous to chartaceous, rarely subcoriaceous, the secondary veins 3—9 on each side of costa and without associated crystal-containing cells; the veinlets distinct below and usually forming striate groups of elongate areoles; domatia frequently present in axils of secondary and also tertiary (and sometimes also higher-order) veins, mainly in the form of tufted hairs or rarely impressed pits or pockets; staminate and pistillate inflorescences compound dichasia, the pistillate inflorescence with fewer branches and flowers, the flowers frequently solitary; bracts narrowly oblanceolate to linear to bristle-like, rarely absent; calyx tube usually (3-) 4-lobed to truncate, usually chartaceous, the lobes distinct, deltoid to linear to oblong; fruits small, less than 15 mm long, the mesocarp thin and lacking cavities or essentially absent; pyrenes 3—11.

Subgenus *Guettardella* is the largest subgenus of *Antirhea* with 28 species extending from southeastern Asia (Malay Peninsula and Hainan) through Malesia to tropical Australia, New Caledonia, Fiji, and Samoa; nearly half of those species are endemic to the Philippines. The subgenus is apparently monophyletic, all member species having leaves supplied by one vascular trace, versus three-trace nodes in subgenera *Antirhea* and *Mesocarpa*. Subgenus *Guettardella* resembles subgenus *Mesocarpa* in having conspicuously dimorphic inflorescences; distinguishing features are given in the above key to subgenera.

KEY TO SPECIES OF *ANTIRHEA* SUBGENUS *GUETTARDELLA*

1. Stipules united at base; leaf blades elliptic; Borneo, Celebes, and Moluccas.
   2. Branchlets glabrous; leaf blades narrowly elliptic, 3—6.5 × 0.8—1.6 cm, glabrous above; ♀ inflorescences 3-flowered; peduncles less than 1 cm long; fruits 4- (5-)seeded; Buru island. 14. *A. buruana*
   2. Branchlets pubescent; leaf blades elliptic, 7.5—12 × 3—5.5 cm, sparsely pubescent above; ♀ inflorescences usually 5- to 11-flowered; peduncles 1—5 cm long; fruits (5-)6- to 11-seeded; E Borneo, S Celebes, and Moluccas. ..... 19. *A. hexasperma*
1. Stipules free at base or, if briefly united then leaf blades ovate; Malay Peninsula to Hong Kong, Philippines, Australia, and Samoa.
   3. Leaf blades to 4 cm long; domatia absent.
      4. Leaf blades chartaceous, 0.7—2.2 × 0.4—1 cm, acuminate to acute at apex; ♂ inflorescences

3- to 6-flowered; peduncles less than 1 cm long; calyx lobes oblong-deltoid, 0.5—1.4 mm long; ♂ corolla tube 5—7 mm long; disc pubescent; ♀ corolla tube to 3.5 mm long; Ilocos Norte and Ilocos Sur Provinces, Luzon, Philippines. .... 24. *A. microphylla*

4. Leaf blades coriaceous, 1.5—4 × 0.8—2.2 cm, emarginate to retuse; ♂ inflorescence (1-) 3- to 25-flowered; peduncles more than 1 cm long; calyx lobes deltoid, 0.2—0.6 mm long; ♂ corolla tube to 3.5 mm long; disc glabrous; ♀ corolla tube to 2.5 mm long; Queensland, Australia. ..... 29. *A. putaminosa*

3. Leaf blades more than 4 cm long, or sometimes shorter; domatia present.
   5. Flowers 3-merous.
      6. Leaf blades elliptic, thin-chartaceous, 7.5—13 × 2.5—5 cm, the secondary veins 7—8 on each side of costa; domatia present; ♂ inflorescences 10- to 22-flowered; floral bracts present; Siargo Island, Philippines. ..... 36. *A. ternata*
      6. Leaf blades lanceolate, chartaceous, 5—7.5 × 2—2.5 cm, the secondary veins 3—4 on each side of costa; domatia absent; ♂ inflorescences to 6-flowered; floral bracts usually absent; Palawan, Philippines. ..... 13. *A. bombysia*
   5. Flowers 4- (5-)merous.
      7. Leaf blades glabrous adaxially; ♂ corolla tube 8—13 mm long; ♀ flowers with 3 (rarely 5) style branches; fruits obovoid, usually strongly 3-ribbed; Queensland, Australia. 35. *A. tenuiflora*
      7. Leaf blades pubescent adaxially; ♂ corolla tube to 9 mm long; ♀ flowers with 4 or more style branches; fruits various.
         8. Domatia present as impressed pits, often pubescent.
            9. Stipules gradually acuminate, 1.5 × 1 mm; domatia glabrous; Zambales Province, Luzon, Philippines. ..... 18. *A. foveolata*
            9. Stipules abruptly acuminate to mucronate, 2.5—10 × 2—3 mm; domatia usually pubescent.
               10. Stipules 6—10 mm long; leaf blades ovate or sometimes elliptic, 1.5—5 cm cm broad; petioles 6—20 mm long; calyx lobes oblong to oblanceolate, 2—5 mm long; fruits cylindric-elliptic, somewhat 4-ribbed; Palawan, Philippines. ..... 15. *A. caudata*
               10. Stipules 2.5—3.5 mm long; leaf blades elliptic, 0.7—1.8 cm broad; petioles to 5 mm long; calyx lobes deltoid, less than 1 mm long; fruits globose; Djajapura, New Guinea. ..... 32. *A. sphaerocarpa*
         8. Domatia not as above or absent.
            11. Stipules minutely puberulent to sericeous inside only toward base.
               12. Leaf blades 8.5—13 × 3—4.5 cm; domatia of tufted hairs; secondary veins 8—10 on each side of costa; Flores Island. ..... 9. *A. affinis*
               12. Leaf blades 2—5 × 0.7—2 cm; domatia absent; secondary veins ca. 5 on each side of costa; Bohol Island, Philippines. ..... 28. *A. philippinensis*
            11. Stipules sericeous over interior surfaces.
               13. Disc glabrous.
                  14. Leaf blades densely sericeous beneath, attenuate at base; calyx cupular, truncate to obscurely denticulate or undulate; Philippines. 11. *A. attenuata*
                  14. Leaf blades sparsely puberulent, acute to rounded at base; calyx lobes distinct.
                     15. Stipules valvate; leaf blades ovate, 2—4 cm long; Queensland, Australia. ..... 26. *A. ovatifolia*
                     15. Stipules imbricate; leaf blades not as above, if ovate, then more than 5 cm long.
                        16. Leaf bases acute to cuneate; ♂ inflorescences usually 80- to 146-flowered; calyx lobes obtuse to truncate at apex; ♀ inflorescences 17- to 19-flowered; Papua. ..... 25. *A. multiflora*
                        16. Leaf bases obtuse to rounded to cordate; ♂ inflorescences 10- to 30- (60-)flowered; calyx lobes acute at apex; ♀ inflorescences 6- to 13-flowered; Fiji and Samoa. ..... 21. *A. inconspicua*
               13. Disc pubescent.
                  17. Stipules valvate.
                     18. Leaf bases cordate to rounded; domatia obscure; ♂ inflorescences 3-flowered; style of ♂ flower 4-branched; Talaud Island. 33. *A. talaudensis*

18. Leaf bases acute to obtuse, rarely rounded; domatia distinctly tufted-pubescent.
    19. Leaf blades adaxially appressed-sericeous; calyx lobes oblong to narrowly deltoid, slightly to strongly unequal, the longer pair 0.8—3 mm long; style glabrous or scabrous to papillose.
        20. Calyx lobes narrowly deltoid, acuminate at apex; ♂ inflorescences 7- to 12-flowered; style of ♂ flower glabrous; NE Borneo. ..... 20. *A. inaequalis*
        20. Calyx lobes oblong-deltoid, obtuse to rounded at apex; ♂ inflorescences 2- to 15-flowered; style glabrous to papillose; Hong Kong & Hainan, China. ..... 16. *A. chinensis*
    19. Leaf blades with indument not as above; calyx lobes deltoid, to 0.5 mm long; style minutely papillose; New Caledonia.
        21. Leaf blades 4—7 × 2—3 cm; ♂ corolla to 5 mm long; fruits ellipsoid, obscurely ribbed, to 8 mm long. ..... 22. *A. ioensis*
        21. Leaf blades 7—12.5 × 3—5.5 cm; ♂ corolla 5.5—7 mm long; fruits obovoid to rhomboid, distinctly 4- to 5-ribbed. ..... 31. *A. rhamnoides*

17. Stipules imbricate.
    22. Leaf blades to 3 cm broad, thin-chartaceous to membranaceous, sparsely pubesent beneath.
        23. Stipules gradually acuminate; leaf blades evenly puberulent beneath; tertiary veins arranged in lineolate-reticulate groups; Malay Peninsula. ..... 10. *A. atropurpurea*
        23. Stipules aristate; leaf blades with lustrous indument only over venation beneath; tertiary veins arranged in lineolate, parallel groups; Philippines. ..... 27. *A. paxillata*
    22. Leaf blades usually more than 4 cm broad, if narrower, then densely pubescent beneath; Philippines.
        24. Plant parts hirsute with yellow to golden-brown hairs; domatia of tufted hairs in vein axils; tertiary veins distinctly raised beneath; ♂ inflorescences 5- to 14-flowered; ♀ inflorescences 1- to 3-flowered; ♀ corolla tube 6—7 mm long; fruits 9—12 mm long; seeds 3—4. ..... 34. *A. tayabensis*
        24. Plant parts pubescent but not as above; domatia obscure or of tufted hairs in vein axils; tertiary veins subplane to prominulous beneath; ♂ inflorescences to 9-flowered; ♀ inflorescences (1-) 3- to 4-flowered.
            25. Calyx lobes less than 1 mm long, obtuse; bracts linear, 4—6 mm long; style base sparsely puberulent; ♀ inflorescences 3- to 4-flowered. ..... 30. *A. ramosii*
            25. Calyx lobes deltoid to linear to oblanceolate, more than 1 mm long, acute to acuminate at apex; style glabrous; ♀ inflorescences 1- to 3-flowered.
                26. Secondary veins prominulous above; calyx tubes ca. 1.5 mm long; bracts to 1.6 mm long; ♀ flowers solitary; corolla glabrous inside; fruits sparsely hirtellous, 3-ribbed; pyrenes 3. ..... 23. *A. livida*
                26. Secondary veins subplane above; calyx tubes ca. 0.6 mm long; bracts 2.4—5 mm long; ♀ flowers 1—3 per inflorescence; corolla glabrous to pubescent toward base inside; fruits not as above; pyrenes usually more than 3.
                    27. Leaf blades densely pubescent beneath, rounded to truncate or sometimes shallowly cordate at base; domatia obscure or of tufted hairs in vein axils; bracts linear to oblanceolate or sometimes acicular, 4—5 × 0.5—1 mm; fruits tomentose, 4—5 mm long. ..... 12. *A. benguetensis*
                    27. Leaf blades sparsely pilose beneath, acute to obtuse at base; domatia distinct in vein axils; bracts usually acicular or rarely linear, to 2.4 × 0.3 mm; fruits sericeous, 7—10 mm long. ..... 17. *A. edanoi*

9. **Antirhea affinis** (Zoll.) Chaw, comb. nov. FIGURE 13a-b

Eriosolena affinis Zoll. Syst. Verz. 116. 1854; Miq. Fl. Ned. Ind. 1(1): 878. 1858.
Guettardella hexasperma sensu Jansen in Blumea 29: 576, *pro parte*. 1984; non sensu typi.

Tree; branchlets 1—1.5 mm broad toward apex, compressed, dispersed- and appressed-puberulent and with scattered, longer, spreading hairs, becoming terete, glabrous, purple-brown, the leaf scars slightly raised, the lenticels pale, conspicuous; stipules imbricate, subcoriaceous, keeled, narrow-deltoid, to 4.5 × 2 mm, gradually acuminate, appressed-pubescent outside but hirtellous on keel, appressed-puberulent inside to densely sericeous toward base, glabrous at margin, the colleters scattered toward center; petioles slender, semiterete to subterete near base, to 12 mm long, to 0.8 mm broad, abaxially appressed-pubescent and sparsely hirtellous, adaxially pubescent; leaf blades elliptic, thin-chartaceous, 8.5—13 × 3—4.5 cm, gradually acuminate at apex, at base acute to acuminate, scattered-puberulent above, more densely so on costa, appressed-pubescent beneath, the indument somewhat longer over costa and lateral veins, the costa slender, subplane above, prominent beneath, the secondary veins subplane above, raised beneath, 8—10 on each side of costa, the intersecondary veins well developed toward distal half of blade, the veinlets impressed above, subplane beneath and forming elongate areoles; domatia of tufted hairs in axils of secondary and sometimes also intersecondary veins; ♂ inflorescences (immature) compound dichasia, 4- or 5-flowered; peduncles slender, to 7 mm long, ca. 0.4 mm broad, appressed-sericeous; bracts subulate to linear, to 1 × 0.2 mm, abaxially pubescent, persistent; calyx tube ca. 0.4 mm high; calyx lobes 4, subulate to oblong, the opposite pairs unequal in length, to 1.2 mm long, 0.4—0.6 mm broad at base, obtuse at apex, pubescent outside; ♀ flowers and fruits not seen.

TYPIFICATION: The type of *Eriosolena affinis* (originally as Thymelaeaceae), is *Zollinger 3209* ♂ (P! holotype), collected from Flores Island (Lesser Sunda Islands) without further locality, July, 1847.

DISTRIBUTION: Presently known only from the type collection.

ECOLOGY AND FIELD NOTES: The single available staminate collection was gathered from a tree, possibly from monsoon forest.

Antirhea affinis is characterized by the unusual distribution of pubescence over adaxial stipule surfaces. The type had been annotated as *Antirhea hexasperma* and placed in *Guettardella hexasperma* by Jansen. While clearly related to that species, *A. affinis* is easily distinguished by its stipules, which are narrowly deltoid and basally free (rather than abruptly cuspidate and basally united), and by the fewer-flowered staminate inflorescences.

10. **Antirhea atropurpurea** (Craib) Chaw ex Wong in Kew Bull. 43: 493. 1988; Wong in Ng, Tree Fl. Malaya 4: 339. 1989.

Timonius sp. Ridley in J. Roy. As. Soc. Str. Br. 59: 115. 1911.
Timonius atropurpureus Craib, Fl. Siam. Enum. 2: 132. 1932; Henderson in J. Mal. Br. Roy. As. Soc. 17: 52, 1939; Chin in Gard. Bull. Sing. 35: 150. 1982.
Timonius hirsutus Ridley in J. Roy. As. Soc. Str. Br. 79: 81. 1918, Fl. Malay Penins. 2: 115. 1923; non Merr. in J. Roy. As. Soc. Str. Br. 77: 242. 1917.

Timonius ridleyi Merr. in J. Arnold Arbor. 18: 132. 1937.
Guettardella atropurpurea (Craib) Jansen in Blumea 29: 571. 1984.

Shrub to small tree; branchlets ca. 1.5 mm broad toward apex, compressed and spreading-sericeous, becoming terete and glabrous, dark brown to nearly

Figure 13. a—b. *Antirhea affinis* (*Zollinger 3209* ♂) a. Adaxial surface of stipule, × 5. b. ♂ inflorescence showing compound dichasium with 5 flower buds (one missing). c—d. *A. attenuata* (*Ramos 1052* ♀). c. Fruit, showing undulate calyx limb, × 5. d. Cross section of fruit showing 4 seed-locules × 5. e—h. *A. bombysia* (*PNH 12400 (Sulit 3873)* ♂). e. Habit, × 0.5. f. Terminal portion of inflorescence showing flower buds, 1 bract, and densely appressed indument, × 2.5. g. Adaxial surface of corolla showing 3 corolla lobes and stamens, × 5. h. Gynoecium and 2 calyx lobes of ♂ flower showing aborted ovary and bifid style. i—m. *A. buruana* (*Taxopeus 468* ♀). i. Habit, × 0.5. j. Branchlet apex showing basally fused stipules, × 5. k. Simple dichasium, × 5. l. Fruit with persistent calyx, × 5. m. Cross section of fruit showing 4 seed locules.

black, the leaf scars raised, the lenticels pale, distinguishable or not; stipules imbricate, chartaceous, deltoid to cuneate, to 5 × 2.5 mm, gradually acuminate and occasionally bifid at apex, scattered-sericeous to hirtellous outside, inside densely sericeous and with scattered colleters on lower half; petioles slender, semiterete, adaxially canaliculate, 4—8 mm long, to 1 mm broad, puberulent to sericeous; leaf blades ovate to oblong-lanceolate to elliptic, thin-chartaceous, 3.5—8 × 1.5—2.5 cm, gradually acuminate at apex, often rounded or sometimes acute at base, scattered-puberulent above, sparsely appressed-sericeous to somewhat densely spreading-sericeous beneath, the indument denser and longer over costa and secondary veins on both surfaces, the costa subplane to prominulous above, raised beneath, the secondary veins subplane to prominulous above, raised beneath, 6—7 on each side of costa, the veinlets often immersed and hardly distinguishable above, plane and conspicuous beneath, forming mostly elongate areoles; domatia of tufted, straight or curled hairs, often obscure; ♂ inflorescences compound dichasia, once to thrice dichotomous, 3- to 7-flowered, spreading-sericeous, the flowers subsessile or the pedicels to 5 mm long; peduncles slender, to 25 mm long, to 0.6 mm broad; bracts linear to bristle-like, to 4 × 0.2 mm, persistent, dispersed-pubescent on both surfaces, more densely pubescent abaxially; calyx tube to 1 mm high, chartaceous, sericeous outside, inside glabrous; calyx lobes 4, narrowly deltoid, occasionally oblanceolate, 2—5 mm long, ca. 0.5 mm broad at base, gradually tapering at apex, scattered-sericeous outside, inside glabrous; abortive ovary obovate, to 0.6 × 0.4 mm, the disc ca. 0.2 mm high, pubescent; ♀ flowers not seen; fruit-bearing peduncle to 2.2 cm long, pubescent; fruits usually solitary, scattered-sericeous, ellipsoid, 3- to 4-ribbed, acute at apex, obtuse to truncate at base, to 8 mm long, to 5 mm diam., subtended by 1—2 bracts, crowned by persistent calyx, the calyx limb sometimes reflexed, the exocarp fleshy, thin; pyrenes 3—4; seeds acute and laterally compressed, pale brown, ca. 4.5 × 0.5—0.7 mm.

TYPIFICATION: In 1911, Ridley noted a sterile collection (*Curtis 2544* from Langkawi, Malay Peninsula) as a species of *Timonius*, and in 1918, with an additional staminate specimen at hand (*Robinson 6229*, also from Langkawi), described this as *T. hirsutus*, a later homonym of *T. hirsutus* Merrill. Craib renamed Ridley's species *T. atropurpureus*, and specified both of the above-mentioned collections as types. The Curtis specimen (SING, n.v.) was designated the [lecto]type by Wong. Merrill's avowed substitute name *Timonius ridleyi* takes the same lectotype.

DISTRIBUTION: Central and western Malay Peninsula.

ECOLOGY AND FIELD NOTES: The few available collections were made mainly on limestone cliffs, ridges, and coasts, at altitudes from near sea level to 250 meters. One flowering staminate specimen was collected in June, the fruiting specimens in August and September.

ADDITIONAL COLLECTIONS: **Thailand.** SURAT: Khao Lak, at 46 km on road Surat-Takuapa, *Smitinand & Sleumer 1187* ♀ (A, K, SING). KAO CHOM LIM: Ampo Kao Kao, *Rabil 309* ♀ (L). **Malaysia.** KEDAH: Langkawi, mainland side of Selat Panchor, opposite N tip of Pulau Timun, *Chin 1834* ♀ (A, L), *Kerr 21738* ♂ (A, L); E coast, *Soepadmo & Mahmud 1255* ♀ (L); Kedah, E end, *Stone 11010* ♀ (L).

This narrow endemic was attributed to *Antirhea chinensis* (as *Guettardella chinensis*) by Bakhuizen van den Brink (1975). The habit, as well as features of indument, inflorescence branching (this often more extensive in *A. chinensis*), and fruit are shared by both species. However, the present species differs from *A. chinensis* in its leaf blades, which are often oblong-lanceolate rather than elliptic, stipules that are gradually acuminate rather than abruptly acuminate, and markedly longer and more narrowly deltoid calyx lobes.

11. **Antirhea attenuata** (Elmer) Chaw, comb. nov. FIGURES 7a-b, 13c-d

Timonius attenuatus Elmer in Leafl. Philipp. Bot. 1: 34. 1906.
Antirhea hirsutiuscula sensu Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 8, 31, *pro parte*. 1909, in Boerl. Ic. Bogor. 4: 113, *pro parte. tab. 335*. 1912; sensu Elmer in Leafl. Philipp. Bot. 3: 1009, *pro parte*. 1911; non sensu typi.
Antirhea hexasperma sensu Merr. Enum. Philipp. Fl. Pl. 3: 540, *pro parte*. 1923; non sensu typi.
Guettardella hexasperma sensu Jansen in Blumea 29: 575, *pro parte*. 1984; non sensu typi.

Habit unknown (tree or shrub?); branchlets ca. 2 mm broad toward apex, compressed and pale-sericeous becoming terete and puberulent to glabrous, dark brown, the lenticels pale, distinct; stipules imbricate, subcoriaceous, keeled, lanceolate, to 4.5 × 3 mm, gradually acuminate toward apex, densely brown-sericeous to tomentose outside, inside pale-sericeous and with colleters near base; petioles slender, adaxially canaliculate, semiterete and somewhat winged by leaf blade, to 15 mm long, 7 mm broad, densely brown-sericeous; leaf blades oblanceolate to obovate, thin-chartaceous, 3.5—9 × 1.5—4.5 cm, acute to gradually acuminate at apex, tapering onto petiole at base, sparsely pubescent above, densely sericeous beneath (especially over venation) with pale, subappressed indument, the costa prominulous above, raised and semiterete beneath, the secondary veins distinguishable above, immersed and hardly distinguishable beneath, spreading, 6—9 on each side of costa, the intersecondary veins well developed, the veinlets forming rectangular areoles; domatia of tufted, straight or curled hairs in axils of secondary and tertiary veins; ♂ inflorescences compound dichasia, 8- to 11-flowered, at anthesis to 4.5 × 2.5 cm, the flowers often sessile and secund; peduncle slender, to 25 mm long, ca. 0.5 mm broad, puberulent; bracts acicular to bristle-like, to 4 × 0.2 mm, puberulent outside, persistent; calyx tube cupular, truncate to obscurely denticulate or undulate, chartaceous, to 1.6 mm high, puberulent outside and on margin, glabrous inside; corolla salverform, the tube to 7.5 mm long, to 1.5 mm diam. at middle, narrower at base, appressed-sericeous outside, inside sericeous only near base, the limb to 4 mm broad, the lobes 4, ovate, to 2 × 1.5 mm, obtuse-rounded at apex, sericeous outside only at very base; stamens 4, inserted ca. 0.5 mm below corolla throat, the anthers subsessile, linear, to 3 × 0.5 mm, their tips exserted; abortive ovary to 0.6 × 0.4 mm, sericeous, 2-loculed, the disc 0.2 mm high, glabrous, the style terete, to 4.5 mm long, to 0.2 mm diam., scabrous to papillose over lower portion, bifid at apex, the slender branches included, to 1.2 mm long, glabrous; ♀ flowers not seen; infructescences once or twice bifurcate with 3—7 fruits, the pedicels 1.5—4 mm long, the fruits dispersed-sericeous, oblong, somewhat laterally compressed or not, 4-ribbed, rounded to truncate at each end, 5—8 mm long, 4—5

mm diam., crowned by persistent calyx and subtended by 1 or 2 bracts, the exocarp thin; pyrenes 4; seeds acute and laterally compressed, brown, to 5 × 0.3 mm.

TYPIFICATION: In describing *Timonius attenuatus*, Elmer specified collections *FB 1867* and *FB 2805* (both from Rizal Province, Philippines) as types; we herewith designate the pistillate specimen *FB 1867* (*Ahern's collector*) in BO(!) the lectotype (isolectotypes at NY!, US!).

DISTRIBUTION: Known as yet only from Rizal Province, Luzon, Philippines.

ECOLOGY AND FIELD NOTES: Flowering specimens have been collected in July. Fruiting specimens have been gathered in the months of July and September. No further information as to habit or habitat is known.

ADDITIONAL COLLECTIONS: **Philippines.** LUZON: RIZAL: Bosoboso, *FB 2805* ♂ (NY, US). Rizal, without further locality: *Ramos 1052* ♀ (G, P, PRC, US, WRSL, Z).

Antirhea attenuata is marked by a cupular and nearly truncate calyx. The species has been regarded by Merrill and Jansen as conspecific with *A. hexasperma*, but the oblong, 4-seeded (rather than laterally compressed, subglobose, and 6- to 11-seeded) fruits suggest specific distinctness. As here interpreted *A. attenuata* is confined to Rizal Province of the Philippines, while *A. hexasperma* is restricted to eastern Borneo, the southern Moluccas, and southwestern Celebes.

12. **Antirhea benguetensis** (Elmer) Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 32. 1909; Elmer in Leafl. Philipp. Bot. 3: 1009. 1911; Merr. Enum. Philipp. Fl. Pl. 3: 540. 1923.

Timonius benguetensis Elmer in Leafl. Philipp. Bot. 1: 35. 1906.
Guettardella microphylla sensu Jansen in Blumea 29: 577, *pro parte*. 1984.

Shrub; branchlets ca. 1.5 mm broad toward apex, compressed, tomentose and with scattered, longer, spreading hairs, becoming subterete and glabrous except above leaf and stipule scars, dark brown to somewhat purplish, the leaf scars raised, the lenticels pale and conspicuous; stipules slightly imbricate, subcoriaceous, deltoid to lanceolate, 4—8 × 2—3 mm, abruptly and sharply acuminate, hirtellous outside, inside densely sericeous toward base, or less so and the hairs shorter toward apex, with scattered colleters toward center; petioles slender, semiterete to subterete near base, adaxially canaliculate, 2—4 mm long, to 1 mm broad, spreading-hirtellous as branchlets, the indument somewhat shorter adaxially; leaf blades angular-obovate to oblong-elliptic, thin-chartaceous to membranaceous, 4.5—11.5 × 2.2—5.5 cm, gradually acuminate at apex, rounded to truncate to sometimes shallowly and unequally cordate at base, sparsely appressed-puberulent above (hirtellous over costa and secondary veins), densely sericeous to hirtellous beneath, the costa canaliculate to subplane above, raised and semiterete beneath, the secondary veins, 6—9 on each side of costa, subplane above, elevated beneath, the veinlets usually forming elongate areoles; domatia of tufted hairs in axils of secondary veins, but sometimes obscure; ♂ inflorescences to twice dichotomously branched, 3- to 7-flowered, at anthesis 1 × 2 cm, the flowers often secund, subsessile; peduncle slender, 10—20 mm long, to 0.3

mm broad, compressed, minutely spreading-puberulent; bracts linear to narrowly oblanceolate, acute, 4—5 × (0.2—) 0.5—3 mm, minutely puberulent on both surfaces, persistent; calyx tube to 1 mm high, puberulent on both surfaces; calyx lobes 4, occasionally somewhat unequal, narrowly deltoid to linear to oblanceolate, chartaceous, 2—4 mm long, 0.5—1 mm broad at base, acute to acuminate at apex, puberulent outside, inside glabrous to sparsely puberulent; corolla salverform, the tube 6—7 mm long, ca. 1 mm diam. at middle, densely appressed-sericeous outside, inside sparsely pubescent near base, the limb 3—4 mm broad, the lobes 4, ovate, 1—1.4 × 0.8—1 mm, acute to obtuse, puberulent outside but scabrous toward margin; stamens 4, inserted ca. 1 mm below corolla throat, the anthers sessile, linear, 3 × 0.4 mm, their tips exserted; abortive ovary to 1.5 mm long, 2-loculed, the style included, 1.2—2.5 mm long, to 0.2 mm diam., glabrous to minutely scabrous, bifid at apex, the slender branches linear, often unequal, to 0.5 mm long, the disc to 0.3 mm high, puberulent distally; ♀ inflorescences 1- to 3-flowered; peduncles (6—) 15—25 mm long, the indument as in ♂ plants; bracts and calyces similar to those of ♂ inflorescences; corolla narrowly infundibular, the tube 4—5.5 mm long, 1—1.5 mm diam. at middle, otherwise similar to ♂ flowers; staminodia resembling stamens but slightly smaller; ovary 2—3 mm long, to 1.5 mm diam., densely spreading-pubescent with pale hairs, (4-) 6- to 8-loculed, the disc ca. 0.2 mm high, puberulent distally, the style 3—5 mm long, ca. 0.5 mm diam., glabrous, 6- to 9-branched at apex, the slender branches usually unequal, to 1.5 mm long, slightly exserted; fruits densely pubescent, oblong-tetragonal to subglobose and laterally compressed, rounded to truncate at both ends, 4- to 7-ribbed, 4—5 mm long, 3—4 mm diam., crowned by persistent calyx and subtended by 2 bracts; pyrenes 4—6 (—9); seeds cylindric, pale brown, acute, ca. 3.5 × 0.4 mm.

TYPIFICATION: *Timonius benguetensis* is typified by *Elmer 6396* ♀ (isotypes at BO!, G!, US!), collected from Twin Peak, Benguet Province, Luzon, Philippines. The holotype in PNH was not seen and is presumed destroyed; all examined isotypes bear the stamp "From the Herbarium, Bureau of Government Laboratories, Manila, P. I."

DISTRIBUTION: Ilocos Sur, Benguet, Bataan, Rizal, and Batangas Provinces, Luzon, Philippines.

ECOLOGY AND FIELD NOTES: Unfortunately, habit and habitat are not reported on any specimens we have seen. Elmer describes the species as "a shrub, 3 m high, its ultimate branches lax and slender. Leaves clustered toward the ends of the branchlets, easily separating or falling and leaving subcircular scars." The majority of flowering and fruiting collections were gathered May to September, except Clemens's specimen (cited below), which bears nearly full-size fruits and was collected in January.

ADDITIONAL COLLECTIONS: **Philippines.** LUZON: ILOCOS SUR: Santa Maria, *Clemens 17927* ♀ (SING). RIZAL: Montalban, *Loher 1413* ♀ (US), *6341* ♀ (BO, US), *BS 12641* ♂ (W); Morong, *BS 1373* ♀ (BO, NY, US); Mt. Susongdalaga, *BS 29343* ♀ (A, BO, US); Pinauisan, *BS 12443* ♂ (A); Rizal, without further locality: *FB 3302* ♀ (BO, NY, SING, US). BATAAN: Corregidor Island, *FB 13226* ♀ (US). BATANGAS: *BS 1865* ♀ (BM, BO, BRI, G, GH, NY, SING). Luzon center, without further locality: *Loher 1415* ♂ (US). Philippines, without further locality: *Loher 6425* ♀ (BO, US).

Most of the specimens here assigned to *Antirhea benguetensis* had been placed by Merrill in *Antirhea microphylla* or in *A. philippinensis*. However, the present species is readily separated by its relatively large and often angular-obovate leaf blades, rather dense and spreading indument over branchlets, ovaries, and lower leaf surfaces, and longer calyx lobes. *Antirhea benguetensis* is similar to *A. livida*, another of Elmer's species, in the pubescence of the leaves and branchlets, but differs in its linear to narrowly oblanceolate bracts and calyx lobes, and densely sericeous fruits with more numerous seeds. The collection *BS 29343*, cited above, is close to *Antirhea microphylla* in leaf blade shape, but in all other respects readily assignable here.

13. **Antirhea bombysia** Chaw, sp. nov. FIGURE 13e-h

Flores trimeri; folia abaxiale aurea-bombycina; bracteae plerumque desunt. Ex affinitate *Antirhea chinensis* (Champ. ex Benth.) Hook. f. sed foliis lanceolatis, costis supra prominentibus, nervis lateralibus untrinque 3—4, et floribus albis differt.

Tree ca. 5 m tall; branchlets 1—1.5 mm broad toward apex, compressed and densely appressed-tomentose to sericeous, becoming terete and glabrous except above stipule and leaf scars, dark brown, the lenticels hardly distinguishable; stipules slightly imbricate, subcoriaceous, lanceolate, 7—9 × 2—3 mm, abruptly long-acuminate (the pointed apex at least twice as long as basal portion), appressed-tomentose outside, inside densely sericeous and with brown colleters scattered centrally; petiole slender, semiterete, adaxially grooved and somewhat winged by leaf blade, to 8 mm long, ca. 6 mm broad, appressed-tomentose; leaf blades lanceolate, chartaceous, 5—7.5 × 2—2.5 cm, gradually acuminate at apex, obtuse or acute at base, scattered-puberulent to nearly glabrous above, densely sericeous beneath with satiny and yellowish to golden indument, the costa prominulous above, elevated and semiterete beneath, the secondary veins subplane above, prominent beneath, spreading, 3—4 on each side of costa, the veinlets subplane above, in groups and forming a striate reticulum, obscure beneath; domatia absent; ♂ inflorescences once to twice dichotomous, (1-) 3- to 6-flowered, ca. 1 cm long (immature), the flowers secund; peduncles slender, compressed, 13—20 mm long, to 0.6 mm broad; bracts usually absent, if present then linear, ca. 1.2 × 0.2 mm, puberulent, persistent; calyx tube to 1 mm high; calyx lobes (2—) 3 (—4), distinctly unequal (one larger), oblong-deltoid, subcoriaceous, 0.5—1.2 mm long, 0.6—0.8 mm broad at base, acute to obtuse at apex, appressed-tomentose outside, less densely pubescent toward apex; corolla salverform, the tube to 5 mm long, to 0.8 mm diam. at middle, tomentose outside, inside serious on lower half, the limb to 4 mm broad, the lobes 3, ovate, to 1.4 × 1.2 mm, obtuse at apex, appressed-tomentose outside but papillose toward margin; stamens 3, inserted ca. 1 mm below corolla throat, the anthers subsessile, linear, 2.2 × 0.5 mm, their tips exserted; abortive ovary obovate, to 1 × 1 mm, appressed-sericeous, the disc 0.2 mm high, pubescent, the style terete, 2.2 mm long, 0.2 mm diam., scabrous, bifid at apex, glabrous, the slender branches included, ca. 0.6 mm long; ♀ flowers and fruits not seen.

TYPIFICATION: *Antirhea bombysia* is typified by *PNH 12400* (*Sulit 3873*) ♂ (A! holotype), collected on Mt. Victoria, Panacan, Aborlan, Palawan Province, Philippines, 18 May 1950.

DISTRIBUTION: Thus far only known from the type locality.

ECOLOGY AND FIELD NOTES: The type collection was made in a rocky, dense, ridge-forest at an altitude of 1000 meters. The staminate flowers are recorded as white.

Antirhea bombysia is one of the most distinctive species of the genus, extraordinary in its 3-merous perianth, the leaf blades abaxially silky, and floral bracts being absent. It resembles *A. chinensis*, but has lanceolate rather than elliptic leaves, an adaxially prominulous costa, fewer lateral nerves, as well as white rather than yellow corollas.

14. **Antirhea buruana** Chaw, sp. nov. FIGURE 13i-m

Ex affinitate *Antirhea hexasperma* (Roxb.) Merr. sed ramulis juvenibus glabris, foliis anguste ellipticis et supra glabris, fructibus oblongo-obovoideis (4—5 seminibus), et inflorescentiis pistillatis semel dichotomis (3 floribus) differt.

Shrub ca. 2 m tall; branchlets ca. 1 mm broad toward apex, compressed, becoming terete, dark brown, glabrous except pubescent above leaf or stipule scars, the leaf scars raised, the lenticels pale, conspicuous; stipules fused basally, lanceolate, abruptly and sharply acuminate, to 4.5 × 2 mm, somewhat keeled, puberulent outside, but glabrous toward margin, inside densely pale-sericeous and with centrally scattered colleters; petioles semiterete and somewhat winged by leaf blade, to 4.5 mm long, 0.6 mm broad, sparsely hirtellous to glabrous, adaxially canaliculate; leaves aggregated toward tips of branchlets, the blades narrowly elliptic, chartaceous, 3.5—6.5 × 0.8—1.6 cm, gradually acuminate at apex, at base acuminate and somewhat decurrent onto petiole, glabrous above, appressed- and scattered-pubescent beneath (somewhat hirtellous over costa and lateral veins), the costa subplane above, elevated beneath, the secondary veins immersed above, prominent beneath, 5—6 on each side of costa, the veinlets hardly distinguishable above, subplane beneath; domatia of tufted and curled hairs in axils of secondary veins; ♂ inflorescences not seen; ♀ inflorescence small (immature), cymose, 3-flowered, at anthesis probably ca. 1 × 1 cm; peduncles stout, compressed, to 6 mm long, 0.6 mm broad, scattered-puberulent to nearly glabrous; bracts linear to bristle-like, 0.8—2 × 0.3 mm, dispersed-puberulent to glabrous, persistent; calyx tube ca. 0.8 mm high, sparsely puberulent; calyx lobes 4, oblong-deltoid, slightly unequal, subcoriaceous, to ca. 0.5 mm long, 0.5 mm broad at base, rounded at apex; corolla narrowly infundibular, the tube ca. 3 mm long, 1 mm diam. at middle, outside appressed-pubescent on upper half, 4-lobed; ovary cylindric, ca. 2 mm long, 1 mm diam., scattered-puberulent, the disc ca. 0.2 mm long, minutely puberulent; fruits (immature ?) oblong-obovoid, 4- to 5-ribbed, ca. 6 mm long, 3 mm diam., crowned by persistent calyx; pyrenes 4—5.

TYPIFICATION: *Antirhea buruana* is typified by *Taxopeus 468* ♀ (L! holotype; isotype at BO!), collected from Fakal, Buru Island, southwestern Moluccas, 30 July 1921.

DISTRIBUTION: Presently known only from the type locality.

ECOLOGY AND FIELD NOTES: The type collection was made on a dry limestone hill, in "alang-alang" (*Imperata* sp. ?) vegetation, at an altitude of 1200 meters. *Antirhea buruana* is recorded as having more or less rose-colored corollas with yellow anthers; the type collection also includes immature fruits.

Antirhea buruana and *A. hexasperma* are the only species of the genus known to have basally fused stipules. However, the present species is readily distinguishable by its glabrous branchlets, narrowly elliptic and adaxially glabrous leaf blades, and fruits that are oblong-obovoid and 4- or 5-seeded. In addition, the pistillate inflorescences are 3-flowered with short, stout peduncles, whereas those of *A. hexasperma* are usually 5- to 10-flowered and the peduncles are longer and more slender.

15. **Antirhea caudata** (Jansen) Chaw, comb. nov.

Antirhea philippinensis sensu Elmer in Leaf. Phillip. Bot. 4: 1327. 1912; non Rolf.
Guettardella caudata Jansen in Blumea 29: 572, *fig. 3*. 1984.
Guettardella microphylla sensu Jansen in Blumea 29: 577, *pro parte*. 1984; non senu typi.

Shrub or tree to 7 m tall; branchlets slender, ca. 1 mm broad toward apex, compressed and tomentose becoming terete and glabrous, dark gray-brown; stipules imbricate, thick-chartaceous, lanceolate, somewhat keeled, 6—10 × 2—3 mm, abruptly and sharply long-acuminate, densely pubescent outside except toward margin, but hirsute on keel and toward apex, inside densely silvery-sericeous and with scattered colleters on lower half of blade; petioles slender, adaxially and distally canaliculate, proximally semiterete to subterete, 6—20 mm long, 0.4—0.8 mm broad, pubescent; leaf blades ovate to sometimes elliptic, thin-chartaceous, (3—) 5—7.5 (—10) × 1.5—3.5 (—5) cm, gradually acuminate at apex, rounded to acute at base, minutely scattered- and appressed-sericeous on both surfaces, more densely so beneath and over venation, the costa slender, subplane above, elevated beneath, the secondary veins canaliculate to subplane, 3—4 (—5) on each side of costa, the veinlets hardly distinguishable above, impressed beneath and forming elongate areoles arranged in reticulate groups; domatia usually present as impressed pits in vein axils, pubescent or not, with wide openings; ♂ inflorescences often simple dichasia, (1-) 3-flowered, the central flower sessile, at anthesis probably to 1 × 1.5 cm, the peduncle slender and compressed, to 45 mm long, ca. 0.5 mm broad, sparsely sericeous; bracts linear to bristle-like, 2.5—5 × ca. 3 mm, sparsely sericeous, persistent; calyx tube to 1 mm high, sericeous outside, inside pubescent basally; calyx lobes 4, oblong to oblanceolate with 3—5 longitudinal veins, chartaceous, 2—5 × 0.5—1.5 mm, acute at apex, sericeous on venation outside, glabrous inside; corolla salverform, the tube to 7 mm long, ca. 1 mm diam. at middle, densely and minutely sericeous outside, inside glabrous to scattered-puberulent basally, the limb ca. 4 mm broad, the lobes 4, ovate, ca. 1.5 × 1.5 mm, acute at apex, minutely sericeous to scabrous toward margin;

stamens 4, inserted ca. 1 mm below corolla throat, the anthers subsessile, linear, 1.8 × 0.3 mm, rounded at base, their tips exserted; abortive ovary to 1 mm long, the disc ca. 0.2 mm high, tomentose, the style filiform, ca. 2.5 mm long, 0.3 mm diam., scabrous, bifid at apex, the slender branches included, unequal; ♀ flowers solitary, resembling ♂, the ovary ovoid, ca. 1.5 mm long, 1 mm diam., densely yellowish sericeous; fruits appressed-puberulent, cylindric-ellipsoid, 4-ribbed, rounded to truncate at each end, to 5 mm long, 4 mm diam., crowned by persistent calyx (to 5 mm high) and subtended by 1 or 2 bracts.

TYPIFICATION: *Guettardella caudata* is typified by *PNH 12315* (*Sulit 3750*) ♂ (L holotype, n.v.; isotype at A!), collected on Victoria Mt. (SW base), Aborlan, Palawan, Philippines, 10 May 1950.

DISTRIBUTION: Palawan, Philippines.

ECOLOGY AND FIELD NOTES: The few available collections were made on rocky sites or seepage ledges along the wooded flanks of rivers, at altitudes from 100 to ca. 300 meters. The wood is reported as hard, heavy, odorless and tasteless, dingy white or brownish in the center, the bark as thin and yellowish except for the smooth gray epidermis. Flowers are said to be subpendent, as are the dark purple fruits. The corolla and calyx are green, at full anthesis turning yellowish, orange-red, or pale pink. The fruit is juicy and obscurely angular. Flowering and fruiting specimens have been gathered in May.

VERNACULAR NAME: "Luñga-luñga" (Tagbanua).

ADDITIONAL COLLECTIONS: **Philippines.** PALAWAN: Mt. Pulgar, Puerto Princesa, *Elmer 13237* ♂ & ♀ (A, BISH, BO, E, G, GH, NY, P, US, W, WRSL). LIPUUN: Lipuun peak, *PNH 91366* (PNH).

The above-cited collections had been attributed to *Antirhea philippinensis* and *Guettardella microphylla* (= *A. microphylla*), but *A. caudata* is distinguishable from those species by the comparatively large and ovate leaf blades with elongate areoles arranged in strongly reticulate groups, by the relatively large calyx lobes with abaxially prominent veinlets, and the fewer-flowered staminate inflorescences. The closest relative of *Antirhea caudata* probably is *A. inaequalis*.

16. **Antirhea chinensis** (Champ. ex Benth.) Forbes & Hemsley in J. Linn. Soc. Bot. 23: 384. 1888; B. L. Robinson in Proc. Amer. Acad. Arts 45: 407. 1910; Merr. & Chun in Sunyatsenia 2: 47. 1934; W. C. Ko in Chun, Fl. Hainanica 3: 339. 1974. FIGURES 1d, 2a-e, 4i-l, 7c-d

Guettardella chinensis Champ. ex Benth. in Hooker's J. Bot. Kew Gard. Misc. 4: 197. 1852; Walp. Ann. 5: 113. 1858; Benth. Fl. Hongk. 158. 1861; Jansen in Blumea 29: 574. 1984.

Shrub or small tree to 6 m tall; branchlets ca. 1 mm broad toward apex, compressed and tomentose, becoming terete and sparsely pubescent to glabrous, dark brown to black, the lenticels pale, conspicuous; stipules valvate, subcoriaceous, lanceolate, abruptly and sharply acuminate, 2.5—6 (—9) × 2—3.5 mm, sericeous outside, inside silvery-sericeous with scattered colleters near base; petioles slender, semiterete and somewhat winged by leaf blade, 3—10 mm long, to 0.8 mm broad, subtriangular near base, tomentose to sericeous; leaf blades

elliptic to narrowly elliptic, chartaceous, (2—) 4.5—9 × 1—3 cm, gradually to abruptly acuminate at apex, acute to obtuse or sometimes rounded at base, minutely scattered-sericeous to nearly glabrous above, densely appressed-sericeous beneath, the hairs silvery to whitish, the costa canaliculate to distally prominulous, elevated beneath, the secondary veins subplane above, raised beneath, 4—5 (—6) on each side of costa, the veinlets immersed and somewhat obscure, forming narrowly elongate areoles; domatia of tufted hairs (sometimes the hairs clavate) in axils of the secondary veins; ♂ inflorescences simple to compound dichasia, 2- to 15-flowered (rarely the flowers solitary), at anthesis 1.5—3 × 1—2 cm, the flowers often sessile, secund on the inflorescence arms; peduncles slender, to 30 mm long, densely sericeous; bracts linear to oblanceolate, acute to obtuse at apex, 1.5—4 × (0.2—) 0.5—1 mm, appressed-sericeous outside, inside sparsely pubescent; calyx tube to 0.6 mm high; calyx lobes 4 (—5), oblong to oblong-deltoid to narrowly obovate, 0.8—2 mm long, 0.5—1.2 mm broad at base, obtuse to rounded at apex, appressed-pubescent outside, less so inside; corolla salverform, the tube 6—9 mm long, to 1.2 mm diam. at middle, densely appressed-sericeous outside with silvery to yellowish hairs, inside scattered-sericeous on lower half, the limb 3.5—5 mm broad, the lobes 4, ovate, to 2 × 1.5 mm, obtuse to rounded at apex; stamens 4, inserted ca. 1 mm below corolla throat, the anthers subsessile, linear, ca. 3 × 0.3 mm, their tips exserted; abortive ovary to 1 mm long, pubescent, the disc ca. 0.2 mm high, pubescent distally, the style filiform, 1.5—2.5 mm long, ca. 0.2 mm diam., scabrous to papillose, bifid at apex, the slender branches included, subequal, to 1.2 mm long, glabrous; ♀ inflorescences (1-) 3-flowered dichasia; peduncles and calyces similar to those of ♂ inflorescences; corolla narrowly infundibular, the tube 3—4.5 (—6) mm long, ca. 1.5 mm diam. at middle, the limb ca. 4 mm wide; staminodia 4, the anthers sessile, linear, ca. 2 × 0.3 mm, included; ovary densely appressed-pubescent, the disc tomentose distally, the style somewhat compressed, to 3 mm long, ca. 0.3 mm diam., glabrous, (2-) 4- (5-)branched at apex, the slender branches subexserted or included, to 0.6 mm long; fruits minutely scattered-sericeous, oblong-obovoid to somewhat rhomboid, 4- (5-)ribbed (the ribs equal or not), obtuse and briefly constricted at apex below the persistent calyx, rounded to truncate at base, 4—7 (—9) mm long, 3—5 mm diam.; pyrenes usually 4 (occasionally 2 or 5); seeds acute and laterally compressed, brown, 4—5 × 0.2 mm.

TYPIFICATION: The type of *Guettardella chinensis* is a Champion collection, gathered on Mt. Gough and Mt. Victoria, Hong Kong, mentioned by Forbes and Hemsley as being at K (holotype, n.v.) and at BM (isotype, n.v.). A Champion specimen (♀) at NY!, collected from Hong Kong without further locality, is perhaps another isotype.

DISTRIBUTION: Hainan Island, South of Guangtung ("Kwangtung") Province (i.e., Suwen, Yangkiang, and Taishan Districts), and Hong Kong, China.

ECOLOGY AND FIELD NOTES: Shrubs or small trees with trunk diameters to 14 cm. Common in roadsides, ravines, and stream banks in thickets and forests, on gentle or steep slopes of clay or loam, at altitudes to ca. 500 meters. The bark surfaces are reported as dark green, the flowers as green-yellow to yellow, the

ripe fruits as black to dark purple, or sometimes red. Flowering specimens have been gathered between March and August; fruiting specimens have been collected throughout the year.

VERNACULAR NAME: "Maucha" (Chinese, meaning that this species resembles hairy tea-plant).

ADDITIONAL COLLECTIONS: **China.** HONG KONG: Lantau Is., Tungchung Hang, Tungchung and vicinity, *Taam 1658* ♀ (A, G, NY, US); Kowloon Reservoir, *Hu 7987* ♀ (US); Victoria Peak, Hotung road *Tang 944* ♂ (A); Aberdeen, *Wang 3038* ♀ (NY); Chungchi College, *Hu 7573* ♂ (US); Kauto Hill (Cove Hill), *Hu 6717* ♀ (US); Peak to Taitam Tuk Reservoir, *N. K. Chun 7525* ♀ (NY); Taitam Tuk Reservoir, Shang Chai Wan, *Tso 21712* ♂ (IBSC); Tailong Wan ("Big Wave Bay"), *Taam 2266* ♀ (G, NY, US); Taipo Tsai, Tsingshui Wan ("Clear Water Bay") road, *Hu 10302* ♂ (US); Hong Kong, near Douglas Village, *Bodinier 627* ♂ & ♀ (E, P); Heungshan, Paak Shu La, *Peng 6273* ♀ (NY); Peak Road, *Chun 5058* ♀ (A, E). Hong Kong, without further locality: *Sampson 293* ♂ & ♀ (BM); *Forbes* s.n. ♂ (BM); *Ford* s.n. ♀ (A); *Ford* s.n. ♂ (NY); *Hance 10144* ♂ (BM, P); *Hu 5079* ♀ (US); *Hu 9339* ♀ (US); *Liou 797* ♀ (NY, W); *Taam 1529* ♀ (A, G, NY, US); *Wright 217* ♂ & ♀ (GH); *Wright* s.n. ♂ & ♀ (NY, P). HAINAN. TUNGFUNG: Kancherng Chuenjiow Ling, *Liang 63307* ♀ (E, NY); Chungnga Shan, *Lau 3270* ♀ (A, BISH). CHANGKIANG: Tsatcha Ling, *Lau 1944* ♀ (A, BM, NY, P). BAKSA: *Lau 26536* ♀ (A). YAIHSIEN: *How 70941* ♂ (BISH, NY), *Liang 62444* ♀ (A, NY, IBSC), *63017* ♀ (A, NY), *Wang 33407* ♀ (MO, NY, US); Yangling Shan, *Lau 215* ♂ (A, B, BM, E, NY, US, W), *6270* ♂ (A). LOHTUNG: Chimfung Ling, near Sammowatt Village, *Lau 3510* ♂ (A, BISH), *4962* ♀ (A). POTING: Taiping Gang, *How 72623* ♂ (BM, P); Nanlin Ling, *Wang 33931* ♀ (A, NY, P), *34433* ♀ (A, G, NY); Tungka-Nansheng (= Wenfa Shi), *N. K. Chun & Tso 43663* ♀ (A, BISH, NY), *43754* ♀ (A, BISH, NY); *Tang 437* ♀ (A); North of Poting, *Liang 62433* ♂ (A, B, NY); Taipor, foot of Seven Finger Mt., *Liang 61688* ♂ (A, B, NY, P, US). WANNING: Shinglong, Niouku Ling, *How 71655* ♂ (A); Nanwang Village, *How 73025* ♀ (A, BO, G).

Antirhea chinensis is most similar to *A. atropurpurea* and *A. bombysia*; differentiating characters are discussed under those species.

17. **Antirhea edanoi** Chaw, sp. nov. FIGURES 5g-h, 7e-f, 14

Antirhea livida Elmer primo adspectu maxime simile, sed foliis sparsim adpressi-puberulis, nervis secundariis supra subplanis, inflorescentiis pistillatis semel dichotomis (3-floribus), ovariis pallidentibus adpressi-pubescentibus et 4- vel 5-locularibus.

Habit unknown; branchlets to 1.5 mm broad toward apex, compressed, tomentose with scattered, longer, spreading hairs, becoming terete, sparsely pubescent to nearly glabrous, gray to gray-brown, the lenticels pale, indistinct; stipules slightly imbricate, deltoid, 6—10 × 3—4 mm, abruptly aristate (the arista shorter than or equaling stipule blade), subcoriaceous, densely sericeous on both surfaces, the colleters scattered centrally inside; petioles slender, subtrigonal to terete at base, to 2.3 mm long, 1.2 mm broad, the indument as on branchlets; leaf blades elliptic to oblong-obovate, chartaceous to submembranaceous, (3.5—) 7.5—13.5 × 3—6 cm, abruptly and sharply acuminate at apex, acute or sometimes obtuse at base, sparsely appressed-puberulent above, sparsely pilose beneath (the hairs denser over lateral veins), the costa canaliculate at base to prominulous near blade apex above, elevated beneath, the secondary veins conspicuous, spreading, ca. 8 on each side of costa, subplane above, prominent beneath, the veinlets striate, forming a reticulum of grouped, elongate areoles; domatia of tufted hairs in axils of lateral and tertiary veins; ♂ flowers not seen; ♀ inflorescences simple dichasia of (1—) 3 flowers, the lateral flowers subtended by 1—3 bracts;

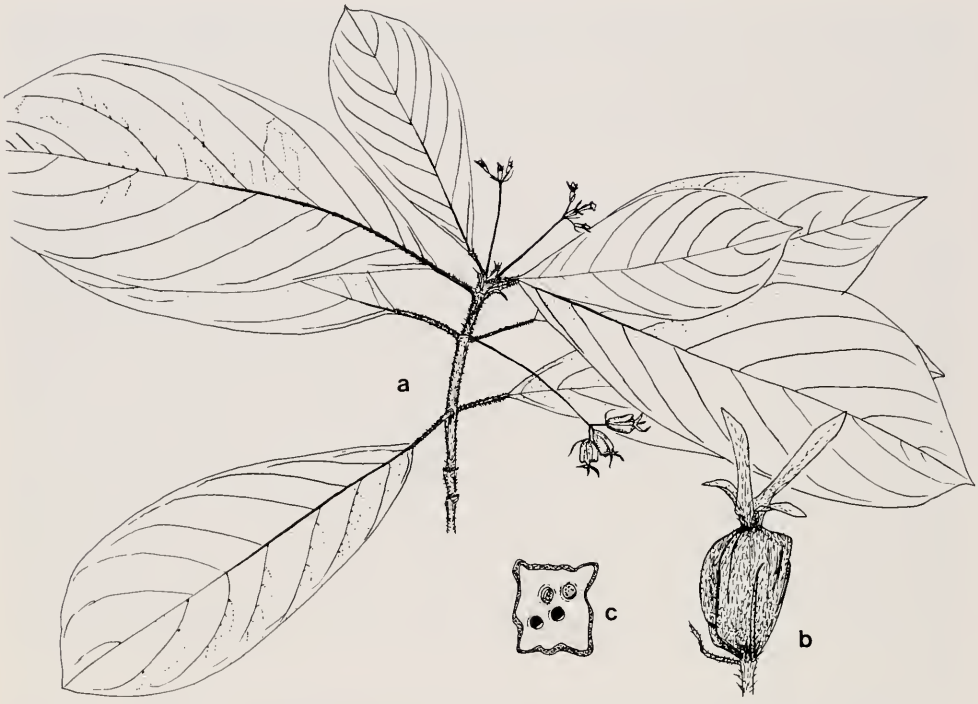


Figure 14. *Antirhea edanoi* (*BS 44015* ♀). a. Habit, × 0.5. b. Fruit with persistent calyx and bract, × 2.5. c. cross section of fruit, × 2.5.

peduncles slender, 20—30 mm long, 0.4—0.6 mm broad, compressed, sericeous; bracts acicular to rarely linear, acute at apex, to 2.4 × 0.1—0.3 mm, sparsely sericeous, persistent; calyx tube ca. 0.6 mm high, inside sparsely pubescent basally; calyx lobes 4, usually unequal in length, subcoriaceous, oblong-deltoid, 1—4 mm long, 0.4—0.8 mm broad at base, acute at apex, sparsely sericeous on both surfaces; corolla salverform, the tube to 5 mm long, ca. 1.2 mm diam. at middle, appressed-pubescent outside, pilose over lower half within, the limb ca. 3.5 mm broad, the lobes 4, ca. 1 × 1 mm, acute to obtuse at apex, scabrous at margin; staminodia 4, inserted ca. 1 mm below throat, the anthers sessile, linear, ca. 2.2 × 0.3 mm, their tips subexserted; ovary oblong-ovoid, somewhat compressed, to 3 × 1.4 mm, pale-tomentose, 4-loculed, the disc ca. 0.2 mm high, distally tomentose, the style cylindric, constricted near base, ca. 4.2 mm long, 0.3 mm diam., sparsely puberulent, 4- (probably to 7-)branched, the branches linear, to 1.5 mm long, subexserted; fruits sericeous, oblong when young, becoming obovoid, (3-) 4- to 5- (7-)ribbed, obtuse at apex and abruptly acute to the persistent calyx, acute at base, 7—10 mm long, 5 mm diam., subtended by 1—2 bracts to 6 mm long; pyrenes 3—7; seeds cylindric, laterally compressed near apex, to 7 × 0.4—0.6 mm, pale brown.

TYPIFICATION: The type of *Antirhea edanoi* is *BS 44015* (*Ramos & Edano*) ♀ (W! holotype; isotypes at A!, B!, BM!, BO!, K!, NY!, SING!, US!), collected from Tawitawi, Sulu Province, Philippines, July-August 1924.

DISTRIBUTION: Known only from the type locality, Sulu Province, Philippines.

ECOLOGY AND FIELD NOTES: Pistillate flowers and fruits have been collected in July and August.

ADDITIONAL COLLECTION: **Philippines.** SULU: Tawitawi, *BS 43943* ♀ (B, G).

The species is similar to *Antirhea livida* in the chartaceous to submembranaceous leaves and pubescent branchlets, but in *A. edanoi* the leaves are sparsely appressed-puberulent above rather than hirtellous, and the secondary veins are subplane adaxially rather than prominulous. In addition, the pistillate flowers of *A. edanoi* are usually arranged in simple dichasia (rarely solitary), and the ovaries are pale appressed-pubescent and 4- to 5-loculed, rather than spreadingly hirtellous and 3-loculed.

18. **Antirhea foveolata** Chaw, sp. nov. FIGURE 15a-c

Species haec ab *Antirhea microphylla* (Bartl. ex DC.) Merr. differt ramulis latioribus, foliis leviter magnioribus, lobis calycis parvi-deltoideis, corollis intus glabris, et praesertim domatiis manifeste foveolatis.

Shrub (?); branchlets ca. 1.5 mm broad toward apex, compressed and tomentose with the hairs reddish brown, becoming terete and glabrous except above leaf and stipule scars, gray-brown, the lenticels hardly distinguishable; stipules subvalvate, subcoriaceous, deltoid-ovate, to 1.5 × 1 mm, acuminate, pubescent outside, inside densely sericeous and with colleters centrally scattered; petioles semiterete, to 2.5 mm long, ca. 0.5 mm broad, hirtellous abaxially, tomentose adaxially; leaf blades elliptic to narrowly obovate, subcoriaceous, acute at apex, at base acute to obtuse, to 2.7 × 1.3 cm, sparsely appressed-puberulent above, the hairs denser beneath, the costa subplane to immersed above, raised beneath, the secondary veins 4—6 on each side of costa, immersed and obscure above, raised beneath, the veinlets obscure above, canaliculate beneath, and forming square areoles; domatia present as impressed pits in axils of secondary veins; ♂ inflorescences once to twice dichotomous, 3- to 5-flowered, at anthesis 2—3 × 2.5—3.5 cm, the flowers sessile or with pedicels to 2 mm long; peduncles slender, compressed, to 10 mm long, 0.6 mm broad, puberulent; bracts acicular, acuminate, ca. 2 × 0.4 mm, puberulent, persistent; calyx tube ca. 1 mm high, appressed-pubescent on both surfaces; calyx lobes 4, deltoid, often unequal in size, chartaceous, 0.3—1.5 mm long, ca. 1 mm broad at base, acute; corolla salverform, the tube to 6.5 mm long, ca. 1 mm diam. at middle, appressed-sericeous outside, inside glabrous, the limb ca. 3 mm broad, the lobes 4, ovate, ca. 1 × 1 mm, acute to obtuse; stamens 4, inserted ca. 1.4 mm below corolla throat, the anthers sessile, linear, ca. 2.6 × 0.3 mm, their tips exserted; abortive ovary to 0.8 mm long, the disc 0.3 mm long, pubescent, the style included, to 1.8 mm long, 0.2 mm diam., glabrous, bifid at apex, the slender branches unequal, to 0.6 mm long; ♀ flowers and fruits not seen.

TYPIFICATION: The type of *Antirhea foveolata* is *BS 4796* (*Ramos*) ♂ (US! holotype), collected from Zambales Province, without further locality, Luzon, Philippines, November-December 1907.

Figure 15. a—c. *Antirhea foveolata* (*Ramos 4796* ♂). a. Habit, × 0.5. b. Adaxial surface of stipule with some trichomes removed to show colleters, × 5. c. ♂ flower, × 5. d—i. *A. ternata* (*BS 34916* ♂). d. Habit, × 0.5. e. Adaxial surface of stipule, × 5. f. Adaxial surface of corolla with 2 stamens removed, × 5. g. Style, × 10. h. Ovary with persistent calyx (dissected) and bract, × 5. i. Abaxial surface of stamen, × 10.

DISTRIBUTION: Known only from the type collection.

The combined features of small, deltoid calyx lobes, and the pit-like, impressed domatia, at once distinguish *Antirhea foveolata* from other Philippine *Antirhea*

species. It resembles *A. microphylla* in its small leaves and flower parts, but differs in the broader branchlets, slightly larger and thicker leaves, and prominent domatia, among other features.

19. **Antirhea hexasperma** (Roxb.) Merr. Enum. Philipp. Fl. Pl. 3: 540. 1923. FIGURE 12h-i

Pyrostria hexasperma Roxb. Hortus Bengal. 83. 1814. nom. nud., Fl. Ind. 1: 403. 1820, ed. 2, 1: 388. 1832.
Polyphragmon trichocaulon Miq. Ann. Mus. Bot. Lugd.-Bat. 4: 241. 1869.
Bobea hirsutiuscula Teysm. & Binn. in Tijdschr. Neederl. Ind. 29: 247. 1867.
Timonius trichocaulon (Miq.) Boerl. Handl. Fl. Ned. Ind. 2: 133. 1891.
Antirrhoea hirsutiuscula (Teysm. & Binn.) Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 31. 1909, in Boerl. Ic. Bogor. 4: 113, *tab. 335*. 1912, in H. Hallier in Beih. Bot. Central. 34(2): 44. 1916; Elmer in Leafl. Philipp. Bot. 3: 1009. 1911.
Bobea hexasperma (Roxb.) Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 7. 1909.
Timonius hirsutiusculus (Teysm. & Binn.) Burck ex Elmer in Leafl. Philipp. Bot. 4: 1329. 1912.
Guettardella hexasperma (Roxb.) Jansen in Blumea 29: 575. 1984.
Guettardella obscura Jansen in Blumea 29: 580, *fig. 4*. 1984.

Small trees to 5 m tall; branchlets ca. 1.5 mm broad toward apex, compressed, appressed-tomentose with scattered, long, spreading, yellow-brown hairs, becoming terete, appressed-puberulent, dark brown, the pale lenticels conspicuous; stipules fused toward base, lanceolate, abruptly cuspidate, 6—10 × ca. 2 mm, hirsute to glabrous toward margin outside, inside densely pale-sericeous; petioles slender, semiterete and canaliculate adaxially, 3—9 mm long, ca. 1 mm broad, abaxially tomentose with scattered, long hairs, pubescent adaxially; leaf blades broad- to oblong-elliptic to rarely angular-obovate, chartaceous, 7.5—12 × 3—5.5 cm, gradually acuminate at apex, obtuse to rounded to sometimes acute at base, sparsely hirsute to hirtellous above (the hairs denser over costa and lateral veins), appressed-puberulent beneath (the hairs longer and coarser over costa and secondary veins), the costa shallowly canaliculate above, raised beneath, the secondary veins subplane above, prominent beneath, 5—7 on each side of costa, the veinlets obscure above, immersed beneath and forming elongate areoles; domatia of tufted hairs in axils of secondary, intersecondary, and tertiary veins; ♂ inflorescences compound dichasia, frequently trifurcate at apex of peduncle, at anthesis to 4 × ca. 5 cm, the flowers 10—74; peduncles slender, compressed, 20—50 mm long, to 1.5 mm broad, appressed-puberulent to hirtellous; bracts linear to bristle-like, 2.5—5 × 0.2—0.5 mm, sparsely pubescent, the bracts sometimes also at distal end of peduncle (when inflorescences trifurcate), one pair stipule-like, ca. 3.5 × 2 mm, another narrower; calyx tube to 0.8 mm high, puberulent outside, nearly glabrous inside; calyx lobes 4 (rarely 3), oblong-deltoid, acute to obtuse at apex, the opposite pairs often unequal in length, to 1 mm long, scattered-puberulent outside; corolla (immature) salverform, the tube to 5 mm long, ca. 1 mm diam. at middle, densely appressed-sericeous outside, inside basally puberulent to glabrous, the limb ca. 3 mm broad, the lobes 4; abortive ovary to 0.8 mm long, pubescent, the disc ca. 0.2 mm high, puberulent, the style filiform, somewhat compressed, to 3 mm long, 0.2 mm diam., usually bifid to rarely simple at apex, included, scabrous; stamens 4, the anthers sessile, linear, ca. 2 × 0.4 mm; ♀ inflorescences of modified compound dichasia, (3-) 5- to 11-flowered, the flowers subsessile to sessile; peduncles to 50 mm long, ca.

2 mm broad, appressed-hirtellous to puberulent; calyces resembling those of ♂ flowers; corolla narrowly infundibular, 3—4.5 mm long, ca. 1.2 mm diam. at middle, densely appressed-sericeous outside, inside pubescent only at base, the limb ca. 4 mm broad, 4-lobed, the lobes ovate, ca. 1.2 × 1.2 mm; staminodia 4, the anthers sessile, linear, ca. 2 × 0.4 mm, included; ovary obovoid, ca. 2 × 1.5 mm, appressed-sericeous, the style cylindric, 4—5 mm long, ca. 0.4 mm diam., glabrous, often 6- (probably up to 11-)branched, the slender branches slightly exserted, unequal, scabrous; fruits appressed-puberulent, orbicular, conspicuously laterally compressed, 5- to 10-ribbed, 4.5—6 mm long, 4—6.5 mm broad, to 4 mm thick, crowned by persistent (and sometimes somewhat reflexed) calyx; pyrenes (5—) 6—11; seeds cylindric, brown, ca. 3—4 mm long, 0.4 mm broad.

TYPIFICATION: Judging from Roxburgh's description, *Pyrostria hexasperma* was based on pistillate (fruiting) as well as staminate material from Honimoa (Saparoea), Moluccas, but no specimens have as yet been located in the Wallich herbarium at Kew, nor is there a Roxburgh drawing of this species at Kew (Sealy, 1956). However, the original description leaves little doubt as to the application of the name, even in the absence of authentic herbarium material. Roxburgh's diagnosis, especially with regard to pedicel, calyx, corolla, and stamens, agrees well with that of *Bobea hirsutiuscula* and *Polyphragmon trichocaulon*. The latter name was based on a *De Vriese* collection from Ceram, and on two Ambon collections: *Teysmann* s.n. and *De Fretes* s.n.. Jansen (1984, loc. cit.) designated a *De Vriese* specimen at L (n.v.) as [lecto]type; another Ceram specimen (♀) at U(!), without collector, bears a label in Miquel's hand, and is possibly an isolectotype. A specimen (♀) at BO(!), labelled "Teysmann & Binnendijk, Saparoea, *Bobea hirsutiuscula*" in Binnendijk's hand, is possibly the holotype of that name, although Teysmann was cited as collector in the protologue. The type of *Guettardella obscura* is *Endert 5397* ♀ (L! holotype; isotype at A!), collected from Kutei, Kombeng, Borneo.

DISTRIBUTION: From eastern Borneo and SW Celebes (Sulawesi), to the southern Moluccas. A Teysmann collection, recorded from Java, probably represents a cultivated specimen.

ECOLOGY AND FIELD NOTES: Unfortunately, habit and habitat are unrecorded in available specimens from the Moluccas. The Bornean and Celebean collections were made on limestone at altitudes to 500 meters. The bark is reported as smooth, the flowers as white. Flowering staminate specimens were collected in July, young fruits in November.

VERNACULAR NAME: "Bau-bau" (Butung Island).

ADDITIONAL COLLECTIONS: **E Borneo.** G. Sekrat, S of Sangkulirang, *Kostermans 5962* ♂ (A, BO, SING). **Celebes.** Butung (Buton) Is., *J. Elbert 2609* ♂ (BO). **Moluccas.** AMBON: Laharoen, *De Fretes (Hort. Bog. 5570)* ♂ (BO, U); Ema, *Teysmann* s.n. ♂ (BO). Ambon, without further locality, *Hort. Bogor. IV E. 50a* ♀ (BO). SAPARUA: *Binnendijk* s.n. ♀ (BO, K); *Hort. Bogor. 14* ♀ (SING); *Hort. Bogor. IV E. 50* ♀ (BO, NY, P, US). **Java,** without further locality [cultivated?]: *Teysmann* s.n. ♀ (K).

The present species is distinct in its basally united stipules and usually compressed-orbicular, (4-) 5- to 10-ribbed fruits. Specimens from eastern Borneo have somewhat smaller leaves, and fruits with 4—5 pyrenes. Merrill stated that *Antirhea benguetensis* is "scarcely distinguishable" from *A. hexasperma,* but we find

them conspicuously dissimilar in characters of the inflorescences, calyx lobes, and fruits. *Antirhea attenuata* also has been confused with *A. hexasperma*, but the former species is densely pale-sericeous on all parts, and has cupular, nearly truncate calyx tubes. The specimen *Lack & Grimes 1757* ♂ (K!), collected from east-central Celebes and having basally connate stipules closely resembles *Antirhea hexasperma*, but the smaller leaves (to 5 cm long) with shiny yellowish indument beneath, and the fewer-flowered (2 to 5) inflorescences are distinctive.

20. **Antirhea inaequalis** Chaw, sp. nov. FIGURE 16

Guettardella obscura sensu Jansen in Blumea 29: 80, *pro parte*, *fig. 4*. 1984; non sensu typi.

Species insignis lobis calycis anguste oblongo-deltoideis et in paribus inaequalibus (praesertim in floribus ad furcas inflorescentiarum); differt a *Antirhea hexasperma* (Roxb.) Merr. stipulis basaliter libris; a *A. caudata* inflorescentiis dichotomis vel trichotomis (7- vel 12-floribus).

Tree ca. 7 m tall; branchlets ca. 1.5 mm broad toward apex, compressed, appressed-pubescent and with scattered, longer hairs, becoming terete, glabrous, brown-black, the pale lenticels obscure; stipules valvate, subcoriaceous to chartaceous at margin, narrowly deltoid to lanceolate, somewhat keeled, to 8 × 3 mm, gradually to abruptly and sharply acuminate at apex, brown-hirtellous outside, inside pale-sericeous and with scattered colleters; petioles slender, adaxially canaliculate, semiterete to subterete at base, 4.5—9 mm long, to ca. 1 mm broad, the indument as on young branchlets; leaf blades elliptic to broadly elliptic, occasionally ovate, thin-chartaceous, 5—7.5 × 2.5—4 cm, acuminate at apex, at base acute to obtuse to sometimes rounded, sparsely appressed-pubescent above (the hairs denser toward the base of costa), sparsely appressed-sericeous beneath (the hairs denser and longer over costa), the costa slender, canaliculate near base to subplane toward apex above, semiterete and raised beneath, the secondary veins subplane above, prominent beneath, 6—8 on each side of costa, the veinlets subplane to immersed above, prominulous beneath and forming elongate areoles arranged in distinct groups; domatia of tufted, straight or curled hairs in axils of secondary and tertiary veins; ♂ inflorescences compound dichasia, 7- to 12-flowered, at anthesis probably to 1.5 × 2 cm; the flowers usually sessile and secund; peduncles slender, to 30 mm long, ca. 1 mm broad, subspreading-sericeous; bracts nearly linear, 0.5—3 × ca. 0.2 mm, sparsely pubescent, persistent; calyx tube to 0.5 mm high, the lobes 4, narrowly oblong-deltoid, the opposite pairs usually unequal in length (particularly in flowers at inflorescence nodes), 0.3—3 mm long, 0.4—0.8 mm broad at base, gradually acuminate at apex, scattered-sericeous outside, inside sparsely pubescent near base; corolla salverform, the tube to 6 mm long, ca. 1 mm diam. at middle, appressed-puberulent to sericeous outside, inside sparsely sericeous over lower half, the limb ca. 3 mm broad, the lobes 4, ovate, to 1.2 × 1 mm, acute at apex, sericeous to scabrous at margin; stamens 4, inserted ca. 1 mm below corolla throat, the anthers subsessile, linear, to 1.6 × 0.4 mm, their tips exserted; abortive ovary to 0.5 mm long, scattered-sericeous, 2-loculed, the disc ca. 0.2 mm high, pubescent, the style filiform, to 2 mm long, ca. 0.1 mm diam., glabrous, bifid at apex, the slender branches

Figure 16. *Antirhea inaequalis* (*SAN A4623* ♂). a. Habit, × 0.5. b. Adaxial surface of stipule with trichomes removed to show colleters, × 5. c. Terminal flower and one lateral branch of compound dichasium, × 5. d. Abaxial surface of subsessile stamen, × 10. e. Style of ♂ flower, × 10. f. Ovary and persistent calyx lobes (2 removed) showing pubescent disc, × 10.

included, to 0.6 mm long, slightly unequal in length, glabrous; ♀ flowers and fruits not seen.

TYPIFICATION: *Antirhea inaequalis* is typified by *SAN A4623* (*G. H. S. Wood*) ♂ (L! holotype; isotype at SING!), collected from Gomantong Caves Hill, 0.25 mi. E of Bumbulud summit (edge of Libingpayu hole), Kinabatangan District, NE Borneo, 22 July 1954.

DISTRIBUTION: Known as yet only from the type locality.

ECOLOGY AND FIELD NOTES: The type collection was gathered at an altitude of ca. 170 meters.

This taxon is remarkable in its calyx lobes, which are narrowly oblong-deltoid and usually composed of long and short pairs; that feature is particularly appar-

ent in the flowers located at inflorescence dichotomies. *Antirhea inaequalis* is readily distinguishable from *A. hexasperma* (including *Guettardella obscura*) by the basally free stipules. *Antirhea inaequalis* is similar to *A. caudata* in its thin-chartaceous leaf blades and unequal calyx lobes, but in the latter species the blades are usually ovate, and the calyx lobes oblong to oblanceolate with distinct longitudinal veinlets. As to the staminate inflorescences, there can be little confusion; those of *A. caudata* are at most only once dichotomous with as many as 3 flowers.

21. **Antirhea inconspicua** (Seem.) Christophersen in Bishop Mus. Bull. 128: 202 (as *Antirrhoea*). 1935; A. C. Smith in op. cit. 141: 140 (as *Antirrhoea*). 1936; Parham, Pl. Fiji Isl. 187 (as *Antirrhoea*). 1964, ed. 2. 264 (as *Antirrhoea*). 1972; S. Darwin in Allertonia 2: 8. *fig. 1, B*. 1979; A. C. Smith & S. Darwin in A. C. Smith, Fl. Vit. Nov. 4: 154. *fig. 62C & D*. 1988. FIGURE 12n

Vangueria ? (an gen. nov.?) Seem. in Bonplandia 9: 257. 1861; A. Gray in Bonplandia 10: 36. 1862.
Vangueria ? sp. Seem. Viti, 438. 1862.
Coffeacea Seem. in Bonplandia 10: 296. 1862, Viti, 438. 1862.
Guettarda inconspicua Seem. Fl. Vit. 131. 1866; Drake, Ill. Fl. Ins. Pacif. 4: 192. 1890; Gillespie in Bull. Bishop Mus. 91: 29. *fig. 32*. 1932.
Guettarda vitiensis A. Gray in Proc. Amer. Acad. Arts 5: 319. 1862; Seem. Fl. Vit. 131. 1866; Drake, Ill. Fl. Ins. Pacif. 4: 192. 1890; nom. nud.
Guettardella inconspicua (Seem.) Jansen in Blumea 29: 576. 1984.

Shrub or tree to 10 m tall; branchlets to 2 mm broad toward apex, compressed, appressed-puberulent to hirtellous, becoming terete, glabrous, dark brown, the pale lenticels conspicuous; stipules slightly imbricate, chartaceous, lanceolate, 5—7 × 2—3 mm, abruptly and sharply acuminate, pubescent outside, inside sericeous, with scattered colleters except toward apex; leaves opposite (sometimes 3 in a whorl); petioles slender, semiterete, 4—8 mm long, 0.5—1 mm broad, appressed-pubescent to hirtellous; leaf blades usually ovate to lanceolate to elliptic, rarely somewhat pandurate, chartaceous to membranaceous, 5—10 (—15) × 2.2—5 (—7) cm, somewhat abruptly acuminate at apex, at base rounded to cordate to sometimes obtuse, scattered-puberulent to nearly glabrous above, scattered-pubescent beneath (somewhat hirtellous over venation), the costa slender, subplane to distally prominulous above, elevated beneath, the secondary veins subplane to canaliculate above, raised beneath, 7—9 on each side of costa, the veinlets forming square and polygonal areoles; domatia indistinct, of tufted hairs in axils of lateral and sometimes also tertiary veins; ♂ inflorescences compound dischasia or thrysoid, 10- to 30- (60-)flowered, at anthesis to 2.5 × 1.5 cm, the flowers often sessile and secund on inflorescence arms; peduncles slender and compressd, to 30 mm long, ca. 0.5 mm broad, appressed-puberulent; bracts narrowly lanceolate to linear, acute, to 6 × 0.5 mm, puberulent, persistent, sometimes also present near distal end of peduncle when inflorescence is thyrsoid, one pair stipule-like, to 3 × 2 mm, another narrower; calyx tube to 1 mm high, the lobes subequal, oblong-deltoid, ca. 0.5 mm long, to 1 mm broad at base, acute at apex, chartaceous to membranaceous, sparsely puberulent outside, inside glabrous; corolla salverform, the tube 6—9 mm long, ca. 1 mm diam. at middle, appressed-puberulent outside, inside pubescent basally, the limb to 4 mm broad, the lobes 4, ovate, ca. 1 × 1 mm, obtuse at apex; stamens 4, the anthers inserted ca. 1 mm below corolla throat, subsessile, linear, ca. 2 × 0.3 mm, their tips

exserted; abortive ovary ca. 0.5 mm long, pubescent, the disc to 0.2 mm high, glabrous, the style compressed, to 1.5 mm long, glabrous, bifid at apex, the slender branches included, unequal, to 0.8 mm long; ♀ inflorescences compound dischasia or thyrsoid, 6- to 13-flowered, at anthesis to 2.5 × 1.5 cm, the flowers often sessile and secund on inflorescence arms; peduncles to 40 mm long, ca. 0.5 mm broad; bracts and calyces resembling those of ♂ flowers; corolla narrowly infundibular, the tube 3—5 mm long, to 1.5 mm diam. at middle, appressed-puberulent outside, inside puberulent basally, the limb to 4 mm broad, the lobes 4, ca. 1.2 × 1 mm; staminodia 4, the anthers subsessile, ca. 1.5 × 0.3 mm, included; ovary pubescent, ca. 1.5 × 1 mm, usually 4-loculed, the style to 4 mm long, ca. 0.3 mm diam., glabrous, usually 4-branched at apex, the slender branches exserted, to 1.5 mm long, the stigmas truncate; fruits glabrous when mature, ellipsoid to obovoid, regularly or irregularly (3-) 4- (5-)ribbed, acute to truncate at each end, 4—8 mm long, to 4 mm diam., crowned by persistent calyx and sometimes also base of style; pyrenes 3—5; seeds cylindric, brown, 3—5 × ca. 1 mm.

TYPIFICATION: In publishing *Guettarda inconspicua* Seemann cited *Seemann 257, Storck 893*, and *MacGillivray* s.n., without indicating a type. Christophersen did not specify a lectotype when he made the combination *Antirhea inconspicua*. Gillespie mentioned *Storck 893* as type of *G. inconspicua* while discussing *Guettarda vitiensis*, but he apparently did not intend to designate a lectotype. *Seemann 257* ♂ was designated lectotype by Smith and Darwin (loc. cit.) (K lectotype, n.v.; isolectotypes at BM!, G!, GH!, P!, W!). The lectotype was collected on Ovalau in 1860. Gray's name *Guettarda vitiensis* was based on a *United States Exploring Expedition* collection, cited below.

DISTRIBUTION: Futuna Island, Fiji, and Western Samoa.

ECOLOGY AND FIELD NOTES: Recorded habitats include dry forests, thickets, coconut plantations, open woods, mangrove swamps on limestone formations, and a variety of coastal habitats, at altitudes from near sea level to 500 meters. The corolla tubes are recorded as red to dull red, the throats and limbs as pale yellow, and the fruits as orange to red and somewhat juicy. Flowering and fruiting occur between July and April.

VERNACULAR NAMES: Fiji: "Kandrage," "Tambutasia" (Lau language, A. C. Smith, 1936, loc. cit.), and "Kau lobo" (Seem.).

ADDITIONAL COLLECTIONS: **Fiji.** MAMANUTHAS: Nggalito Island, *O. & I. Degener 32218* ♂ (B, BISH, E, NY). VITI LEVU: MBA: Lautoka, N of Lomolomo, *O. Degener & Ordonez 13633* ♀ (A, BISH, BRI, NY, US); Vatia, W of Tavua, *O. Degener 14977* ♀ (A, BISH, NY, US). NANDRONGA & NAVOSA: near Koro Nasingana, *H. B. R. Parham 130(b)* (BM); Viti Levu, without further locality: *U. S. Expl. Exped.* ♀ (GH, NY). OVALAU: *Storck 893* ♀ (BM, GH, W). KORO: E coast, *A. C. Smith 1039* ♀ (BISH, BO, GH, NY, P, US). VANUA LEVU: MATHUATA: Seanggangga, *DA 13934* ♀ (BISH, BRI). THAKAUNDROVE: S coast near road to Salt Lake, *DA 16829* ♀ (BISH); Maravu, near Salt Lake, *O. Degener & Ordonez 14240* ♀ (A, BISH, US); NGAU: *MacGillivary* s.n. (BM) p.p., *MacGillivary* s.n. ♀ (W). MOALA: near Maloku, *A. C. Smith 1330* ♀ (BISH, BO, GH, NY, US). KAMBARA: *A. C. Smith 1269* ♀ (BISH, BO, GH, NY, US). FULANGA: *A. C. Smith 1131* ♂ (BISH, BO, GH, NY, US). Fiji, without further locality: *Horne 385* ♀ (GH); *Horne 401* ♂ (GH). **Horne Is.** FUTUNA: *Hoff 4182* ♀ (US). **Samoa.** SAVAII: near Fagalele, *Christophersen 3396* ♀ (B, BISH, NY, P); between Salailua and Lataitai, *Christophersen 2649* ♀ (B, BISH, BO, NY); between Salailua and Lataiuta, *Christophersen 3011* (BISH, US); near Apopo, *Rechinger 1049* (W); near Lealutelo, *Rechinger 1179* ♀ (W); near Safune, *Christophersen & Hume 2428* (BISH);

Lealetele, *Christophersen & Hume 2470* ♂ (BISH, NY); between Saloto and Manase, *Christophersen 3472* ♀ (A, BISH, BO, US). Savaii, without further locality: *Rechinger 1148* ♀ (W); *Rechinger 4486* ♀ (W); *Vaupel 84* ♂ & ♀ (B, MO, US, W). APOLIMA: *Rechinger 820* (W). UPOLU: Lefaga, Falese'ela, *Bristol 2318* ♂ (BISH, GH, US); near Moamoa, *Rechinger 57* ♂ (W); near Laulii, *Rechinger 795* (W); between Siumu and Poutasi, *Whistler W3862* ♀ (BISH, G); northwest of Amaile, *Whistler W1839* ♀ (US); E end of Upolu, *Whistler W1874* ♀ (B, BISH, US). NAMU'A: *Whistler W3945* ♂ (BISH, US). NU'UTELE: *Whistler W4020* ♀ (BISH). Samoa, W side of Mt. Mariota near Tanumalala, *Whistler W764* ♀ (A, B, BISH, US); Samoa, without further locality: *Whitmee* s.n. (BM, GH, MEL).

Antirhea inconspicua is the easternmost species of the genus. Its geographical range partially overlaps that of *A. smithii*, but their leaf textures, blade outlines, bracts, and fruit sizes are strikingly different. *Antirhea multiflora* is likely the closest ally of *A. inconspicua*, although they are quite isolated geographically; shared characteristics include leaf blade texture, inflorescence branching pattern, fruit size, and flowering period. Differences include shape of the leaf base, number of flowers in staminate and pistillate inflorescences, and the number of pyrenes per fruit.

22. **Antirhea ioensis** (Baill.) Chaw, comb. nov. FIGURES 5d-f, 7g-h, 12f-g

Guettarda ioensis Baill. in Adansonia 12: 242. 1879; Guillaumin in Notul. Syst. (Paris) 1: 195. 1912, in Arch. Bot. (Paris) 3(5): 20. 1929, Fl. Nouv. Calédon. 331. 1948.

Shrub or tree to 4 m tall; branchlets ca. 1.5 mm broad toward apex, compressed and densely to sparsely puberulent, becoming terete and glabrous, gray to dark gray; lenticels pale; stipules valvate, chartaceous, lanceolate, 4—10 × 2—3 mm, gradually acuminate, puberulent outside, inside densely sericeous and with centrally scattered colleters; petioles slender, semiterete to subterete at base, to 7 mm long, to 1 mm broad, sparsely puberulent, the indument slightly longer abaxially and appressed; leaf blades elliptic to sometimes obovate, chartaceous to subcoriaceous, gradually acuminate at apex, usually acute to sometimes obtuse at base, 3.5—4 × 1.8—3 cm, minutely scattered-puberulent to nearly glabrous above, the indument denser beneath, especially over costa and secondary veins, the costa slender, subplane to prominulous above, raised beneath, the secondary veins 3—5 on each side of costa, plane to prominulous above, raised beneath, the veinlets often obscure, usually forming reticulate groups of lineolate areoles; domatia usually of tufted hairs, or sometimes also membranous pockets in axils of secondary veins; ♂ inflorescences simple dichasia (sometimes one of the branching arms missing), 2- to 3-flowered, at anthesis probably ca. 1 × 1 cm, the flowers sessile or the pedicels to 0.5 mm long; peduncle compressed, 6—10 mm long, to 1 mm broad distally, minutely puberulent; bracts acicular, acuminate, to 3 × 1.5 mm, persistent; calyx cupular, ca. 2 mm high, 4-lobed, the lobes somewhat unequal in size, deltoid, chartaceous, 0.2—1 mm long, ca. 1 mm broad at base, acute at apex, puberulent on both surfaces but the indument laxer inside; corolla salverform, the tube ca. 5 mm long, 1 mm diam. at middle, puberulent outside, inside villous only near base, the limb ca. 4.5 mm broad, the lobes 4, ovate, ca. 1.4 × 1 mm, acute at apex, scattered-puberulent outside, inside papillose; stamens 4, inserted ca. 1.5 mm below corolla throat, the anthers sessile, linear, ca. 2.5 × 0.6 mm, their tips exserted; abortive ovary obovoid, ca. 1 mm long, 1 mm diam., 2-loculed, the disc to 0.3 mm high, puberulent, the style

included, cylindric to somewhat angular, to 2.2 mm long, ca. 0.5 mm diam., minutely baculate to papillose, bifid at apex, the slender branches filiform, slightly unequal, to 0.7 mm long; ♀ inflorescences not seen; fruits solitary, minutely puberulent, ellipsoid, obscurely ribbed, 7—8 mm long, 4—5 mm diam., crowned by persistent calyx ca. 2 mm long; pyrenes 4 or 5; seeds cylindric, pale brown, acute and laterally compressed distally, 4 × 0.5 mm.

TYPIFICATION: *Guettarda ioensis* is typified by *Balansa 2392* ♂ (P holotype?, n.v.; isotype at Z!), collected from Io Valley, New Caledonia, 28 December 1869.

DISTRIBUTION: Endemic to New Caledonia.

ECOLOGY AND FIELD NOTES: The few available specimens were collected at altitudes from 33 to 300 meters. The leaves are reported as soft, dark green above, the flowers as white. Staminate specimens have been collected in December and January; a fruiting specimen was gathered in July.

ADDITIONAL COLLECTIONS: **New Caledonia.** Népoui Peninsula, bluffs above ocean, *McMillan 5048* ♀ (A); Route de l'Hermitage, *McKee 3691* ♀ (A).

Baillon thought the leaves on the type collection to be immature; leaves of the other examined specimens are thicker in texture and not aggregated at branchlet tips. Morphologically, *Antirhea ioensis* is close to *A. rhamnoides*, but in the former species the petioles, leaf blades, peduncles, corolla tube and style branches (staminate flowers), and fruits are distinctly smaller. Furthermore, *Antirhea ioensis* has an ellipsoid (rather than rhomboid) and obscurely (versus strikingly) ribbed fruits.

23. **Antirhea livida** Elmer in Leafl. Philipp. Bot. 4: 1327. 1912; Merr. Enum. Philipp. Fl. Pl. 3: 540. 1923. FIGURE 12j-k

Guettardella livida (Elmer) Jansen in Blumea 29: 576. 1984.

Shrub to 5 m tall; branchlets ca. 1.5 mm broad toward apex, compressed, spreading-tomentose and with scattered, longer hairs, becoming subterete and glabrous, gray-brown, the pale lenticels conspicuous; stipules imbricate, subcoriaceous, lanceolate, 6—12 × 1.5—3 (—4) mm, gradually to abruptly acuminate at apex, hirtellous outside, inside pale-sericeous with dark brown colleters near base; petioles slender, subterete to terete at base, 4—8 mm long, ca. 1 mm broad, indument as on young branchlets; leaf blades elliptic to broadly elliptic, thin-chartaceous, 4—11 × (2—) 3—7 cm, abruptly acuminate at apex, subtruncate to rounded at base, sparsely hirtellous above (the hairs denser over costa and lateral veins), subappressed-sericeous beneath (hirtellous over venation), the costa subplane to distally prominulous above, prominent beneath, the secondary veins prominulous above, raised beneath, 5—8 on each side of costa, the veinlets hardly distinguishable above, conspicuous beneath and forming both elongate and square areoles; domatia of tufted hairs in axils of secondary veins; ♂ inflorescences cymose, 3-flowered, at anthesis to 2.5 × 1.5 cm, the central flower sessile; peduncles slender, to 15 mm long, ca. 0.5 mm broad, hirtellous; bracts usually absent or sometimes bristle-like, 1.2—1.6 × 0.1 mm, pubescent, persistent; calyx tube to 1.5 mm high, hirtellous outside (near base the hairs clavate or pointed),

the lobes 4, slightly unequal in length, narrowly deltoid, 2—3 mm long, to 0.7 mm broad at base, sharply acuminate, hirtellous outside, inside sericeous; corolla (immature) salverform, the tube 5.5—6.5 mm long, ca. 1 mm diam. at middle, constricted near base, appressed-pubescent outside, inside glabrous, the lobes 4, ovate; stamens 4, inserted ca. 1 mm below corolla throat, the anthers subsessile, linear, ca. 2 × 0.5 mm, their tips exserted; abortive ovary obscure, ca. 0.5 mm long, densely yellowish hirtellous, 2-loculed, the disc 0.1 mm high, pubescent, the style slender, to 2 mm long, bifid at apex, glabrous, the slender branches included, ca. 1.7 mm long; ♀ flowers (immature) solitary; fruit-bearing peduncle slender, to 2 cm long, sparsely hirtellous; fruits ellipsoid, to 10 mm long, 5 mm diam., 3-ribbed, rounded to truncate at apex, acute at base, crowned by persistent calyx and often subtended by one bract; pyrenes 3.

TYPIFICATION: *Antirhea livida* is typified by *Elmer 12968*, collected on Mt. Pulgar of Puerto Princesa, Palawan, the Philippines, April 1911. The holotype in PNH is presumed destroyed. The type collection includes both pistillate and staminate specimens; we herewith designate the pistillate specimen at P(!) the lectotype (isolectotype at BISH!). Staminate specimens with this collection number are at A!, BISH!, BM!, BO!, E!, G!, GH!, NY!, PRC!, US!, W!, WRSL!, and Z!.

DISTRIBUTION: Known as yet only from the type locality.

ECOLOGY AND FIELD NOTES: The type collection was made in a humid forest at an altitude of ca. 80 meters. The wood is reported as solid and hard, the bark scaling in very thin plates, or smooth; the main branches are widely spreading and ultimately much ramified. The leaves are recorded as clustered, rotately spreading, diverse in size, soft-membranous, and deep green above; the mature fruits as shining-lividus, juicy, and angular.

Elmer's field notes are erroneous in describing the inflorescences of *Antirhea livida* as terminal. He described the lateral (staminate) flowers as "subtended by bristly hair-like bracts," and the fruits as "subtended by the persistent bracts," but in both inflorescences the bracts are frequently missing. The present species resembles *Antirhea benguetensis* and *A. tayabensis;* under those species we discuss the distinguishing characters.

24. **Antirhea microphylla** (Bartl. ex DC.) Merr. Enum. Philipp. Fl. Pl. 3: 540. 1923. FIGURE 17a-h

Guettarda microphylla Bartl. ex DC. Prodr. 4: 457. 1830; Fern.-Vill. Nov. App. 109. 1880.
Guettardella microphylla (Bartl. ex DC.) Jansen in Blumea 29: 577. 1984.

Shrub (?); branchlets ca. 1 mm broad toward apex, often compressed (sometimes trigonal) and appressed-tomentose (sometimes with scattered, longer hairs), becoming terete and glabrous except above stipules and leaf scars, the leaf scars distinctly raised; stipules slightly imbricate, subcoriaceous, somewhat keeled or not, lanceolate to deltoid, 1.5—3 × 1—2 mm, gradually acuminate, puberulent to hirtellous on keel outside, inside pale-sericeous and with scattered colleters near base; petioles short, slender, semiterete to subterete near base, 1—2 mm long, ca. 0.4 mm broad, pubescent to somewhat hirtellous; leaves opposite or

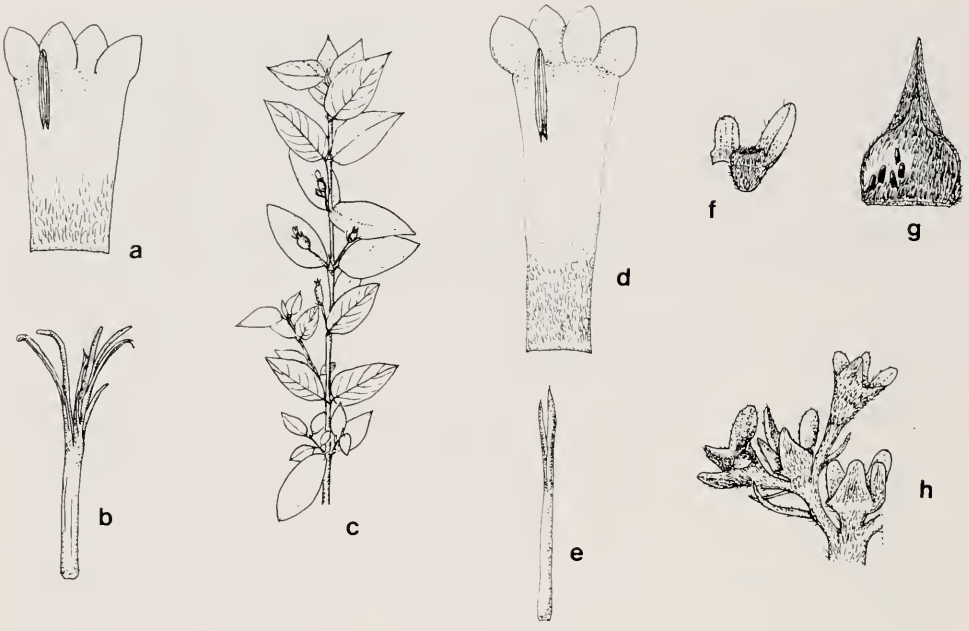


Figure 17. *Antirhea microphylla* (a–c from *BS 33450* (*Ramos*) ♀; d–h from *Haenke* s. n. ♂). a. Adaxial surface of corolla with 3 staminodia removed, × 5. b. Style of ♀ flower, × 5. c. Habit, × 0.5. d. Adaxial surface of corolla with 3 stamens removed, × 5. e. Style of ♂ flower, × 10. f. 2 calyx lobes and ovary, showing pubescent disc, × 5. g. Adaxial surface of stipule with some trichomes removed to show colleters, × 10. h. Terminal flower and one lateral branch of compound dichasium after anthesis, × 5.

sometimes in whorls of 3; leaf blades small, ovate-lanceolate to rarely oblong-elliptic, thin-chartaceous, 0.7—2.2 × 0.4—1 cm, acuminate to acute at apex, at base usually obtuse to truncate to cordate (rarely acute), sparsely pubescent above, appressed-pubescent beneath (the hairs denser on costa and secondary veins), the costa subplane above, raised beneath, the secondary veins subplane to prominulous above, raised beneath, 4—6 on each side of costa, the veinlets hardly distinguishable above, subplane beneath and forming mainly elongate areoles; domatia absent; ♂ inflorescences once or twice dichotomous, at anthesis probably to 1 × 1 cm, 3- to 6-flowered, the flowers often sessile and secund; peduncles slender, to 8 mm long, 0.4 mm broad, pubescent, the rachis pubescent; bracts linear to bristle-like, occasionally oblanceolate, to 2 × 0.3 mm, dispersed-pubescent, persistent; calyx tube to 0.5 mm high, scattered-sericeous outside, inside pubescent only at base; calyx lobes 4, oblong-deltoid, slightly unequal in length, 0.5—1.4 × 0.4—0.6 mm, scattered-sericeous outside, glabrous inside; corolla salverform, the tube 5—7 mm long, to 1 mm diam. at middle, appressed-pubescent outside, inside appressed-sericeous on lower half (the hairs curled), the limb ca. 3.5 mm broad, the lobes 4, ovate, to 1.6 × 1.2 mm, acute at apex, sericeous to papillose at margin outside; stamens 4, sessile, inserted ca. 1 mm below corolla throat, the anthers linear, ca. 2.5 × 0.3 mm, their tips subexserted; abortive ovary to 0.3 mm long, pubescent, 2-loculed, the disc to 0.4 mm high, pubescent, the style filiform, to 2.2 mm long, ca. 0.8 mm diam., glabrous, bifid

at apex, the slender branches included, unequal, to 0.7 mm long; ♀ flowers solitary; peduncles, bracts, and calyx resembling those of ♂ flowers; corolla narrowly infundibular, the tube to 3.5 mm long, ca. 1 mm diam. at middle, in indument and other characters similar to ♂ corollas, the anthers smaller, ca. 1.8 × 0.3 mm, the style to 2.5 mm long, ca. 0.8 mm diam., 6-branched, the slender branches subexserted, unequal, to 1 mm long; fruits (immature) scattered-pubescent, ellipsoid, obtuse to truncate at each end, to 5 mm long, ca. 3 mm diam.; pyrenes probably 6; seeds immature.

TYPIFICATION: *Guettarda microphylla* is typified by a *Bartling* (♂) specimen in the Haenke herbarium (PR! holotype; isotypes at BM (photo!), MO!, PRC!), from Luzon, Philippines. The type collection is likely from Ilocos Norte or Ilocos Sur Provinces, a region that Haenke visited (Steenis, 1950) and from where all other available collections were made.

DISTRIBUTION: Ilocos Norte and Ilocos Sur Provinces, Luzon, Philippines.

ECOLOGY AND FIELD NOTES: Flowers (staminate and pistillate) and young fruits have been gathered in July.

ADDITIONAL COLLECTIONS: **Philippines.** LUZON: ILOCOS NORTE: Burgos, *BS 32890* ♂ (A, US), *33450* ♀ (BM, BO). ILOCOS SUR: Candon, *M. S. Clemens 18683* (SING).

The present taxon has the smallest leaves of *Antirhea* species. It is similar to *A. benguetensis,* under which we discuss differentiating features. Martelino & Edano's collections *BS 35571* ♂ (A!, US!) and *BS 33596* ♂ (BO!), both representing the same taxon, were referred to *A. microphylla* by Merrill, but in both collections the larger leaf blades (3—5 × 2—3 cm) with shiny and yellowish indument over the venation, the presence of domatia, and the more densely flowered inflorescences are distinctly different from the characters we ascribe to *A. microphylla* in a narrower sense. The assignment of those two collections from Capiz Province (Panay, Philippines) remains questionable.

25. **Antirhea multiflora** (Jansen) Chaw, comb. nov.

Guettardella multiflora Jansen in Blumea 29: 578, *fig. 4.* 1984.

Shrub to small tree; branchlets ca. 2 mm broad toward apex, compressed and subappressed-tomentose to hirtellous, becoming terete and glabrous, brown, the pale lenticels conspicuous; stipules imbricate, subcoriaceous, lanceolate, (5—) 8—15 × 3—4 mm, abruptly and sharply acuminate to aristate at apex, tomentose on both surfaces, and with colleters scattered inside except near apex; petioles slender, semiterete to subterete at base, 4—23 mm long, 0.6—1.4 mm broad, tomentose; leaf blades often elliptic to rarely oblanceolate or obovate, membranaceous to sometimes chartaceous, 8—15 × 3—5.5 cm, gradually to abruptly acuminate at apex, at base broadly acute to cuneate, scattered-puberulent to sericeous above (the hairs longer and denser over venation), appressed-puberulent to tomentose beneath (the indument hirtellous and denser over venation), the costa canaliculate near base to subplane or minutely prominulous toward apex, raised and nearly semiterete beneath, the secondary veins subplane to plane above, raised beneath, spreading, 6—9 on each side of costa, the veinlets forming mostly

elongated areoles; domatia often obscure, of tufted, straight or curled hairs in axils of secondary veins when present; ♂ inflorescences compound dichasia to thyrsoid, (24-) 80- to 146-flowered, at anthesis to 5.5 × 4.5 cm, the flowers sessile or with pedicels to 2.5 mm long; peduncles pubescent, slender, to 35 mm long, ca. to 1 mm broad; bracts at distal end of peduncle stipule-like and the opposite pairs slightly unequal, to 3.5 × 2 mm, other bracts linear, to 2.5 × ca. 0.3 mm, spreading-puberulent, persistent; calyx tube to 0.7 mm high, pubescent basally; calyx lobes 4, deltoid to oblong, to 0.5 mm long, to 0.5 mm broad at base, obtuse to truncate at apex, puberulent outside, glabrous inside; corolla salverform, the tube 5—6.5 mm long, ca. 0.6 mm diam. at middle, constricted near base, appressed-puberulent outside, inside villous on the lower half, the limb to 3 mm broad, the lobes 4, ovate, to 1.2 mm long, to 1 mm broad, rounded at apex, puberulent to papillose at margin outside; stamens 4, inserted ca. 0.5 mm below corolla throat, subsessile, the anthers linear, to 2 × 1—1.5 mm, their tips exserted; abortive ovary to 0.5 mm long, ca. 0.3 mm diam., appressed-pubescent, 2-loculed, the disc ca. 0.2 mm high, glabrous, the style terete, to 2.2 mm long, ca. 0.2 mm diam., glabrous, bifid at apex, the slender branches included, slightly unequal, to 1 mm long; ♀ flowers not seen; infructescences trifurcate, thyrsoid, with 17—19 fruits, the fruits often sessile and secund, or on pedicels to 1.5 mm long, scattered-puberulent, ellipsoid, somewhat laterally compressed or not, (4-) 6- to 7-ribbed, rounded at each end, 4.5—5.5 mm long, to 4.5 mm diam., crowned by persistent calyx and subtended by 1 or 2 bracts, the exocarp fleshy, thin; pyrenes (4—) 6—7; seeds cylindric, pale brown, to 3 × 0.6 mm.

TYPIFICATION: *Guettardella multiflora* is typified by *Brass 21936* ♀ (L holotype, n.v.; isotypes at A!, US!), collected at Menapi, Cape Vogel Peninsula of Milne Bay District, Papua, 16 April 1953.

DISTRIBUTION: Southeastern Papua and adjacent islands.

ECOLOGY AND FIELD NOTES: The few available collections were made in the undergrowth of rain forests, in secondary and disturbed lowland hill forests, or in regrowths on reddish limestone soil at 15 to 250 m altitude. The flowers are white or yellow; the ripe fruits are red. Flowering and fruiting probably from September to April.

VERNACULAR NAME: "Umaswakoakora" (Minufia, Dabora).

ADDITIONAL COLLECTIONS: **Papua.** MILNE BAY: Cape Vogel, ca. 3 mi. N of Dabora, *Saunders 151* ♂ (A, BRI, CANB, US). PAPUAN IS.: Madaway Is., *Kairo 211* ♂ (CANB); Normanby Is., inland from Miadeba, *LAE 68898* ♂ (A, BISH, BRI, CANB, E, SING).

The similarity between *Antirhea multiflora* and *A. inconspicua* is discussed under the latter species.

26. **Antirhea ovatifolia** (Jansen) Chaw, comb. nov. FIGURE 2h-j

Guettardella ovatifolia Jansen in Blumea 29: 582, *fig. 3*. 1984.

Shrub or small tree to 5 m tall; branchlets ca. 1 mm broad toward apex, compressed, tomentose to hirtellous, becoming terete, subglabrous, and brown

to dark purple, the lenticels pale, the leaf scars raised; stipules valvate, deltoid to lanceolate, acuminate, 3—5 × 2.5—3.5 mm, subcoriaceous, hirtellous to hirsute abaxially, densely pale sericeous adaxially; petioles slender, subterete, densely sericeous to hirtellous; leaf blades ovate, often chartaceous to membranaceous, 2—4 × 1—3 cm, acute to acuminate at apex, rounded or sometimes cordate at base, sericeous to hirtellous on venation above (the hairs denser over costa and lateral veins), hirtellous beneath, the costa subplane to prominulous above, elevated beneath, the secondary veins prominulous on both surfaces, 6—8 on each side of costa, the veinlets obscure above, subplane beneath, often striate or forming square to rectangular areoles; domatia of tufted indument in axils of secondary veins, the hairs rod-shaped, clavellate and sharply pointed; ♂ inflorescences simple dichasia, sometimes with one branch reduced, 2- or 3-flowered, at anthesis to 2 × 0.8 cm; peduncles slender, minutely sericeous, to 10 mm long, 0.4 mm broad; bracts linear, to 2 × 0.3 mm, acute at apex, scattered-sericeous on both surfaces; calyx tube, ca. 0.6 mm high; calyx lobes 4, charataceous, the opposite pairs slightly to strongly unequal, deltoid to subulate to sometimes narrow-oblanceolate, 0.8—4 mm long, to 0.5 mm broad at base, acute to acuminate at apex; corolla narrowly infundibular, the tube 3—4.5 mm long, 0.8—1.2 mm diam. at middle, appressed-pubescent outside, basally pilose inside, the limb ca. 3 mm broad, the lobes 4, ovate, to 1.2 × 1 mm, obtuse at apex; stamens 4, sessile, the anthers ca. 1.5 × 0.3 mm, their tips exserted; abortive ovary to 1 × 0.8 mm, densely sericeous, 4-loculed, the disc ca. 0.3 mm high, glabrous, the style linear, to 2 mm long, ca. 0.2 mm diam., glabrous, bifid at apex, the slender branches included, to 0.3 mm long; ♀ flowers not seen; infructescences with 3—4 fruits or sometimes fruits solitary; fruits globose to obovoid, somewhat laterally compressed, irregularly 4- or 5-ribbed, 6—8 mm long, 3—5 mm diam., sparsely puberulent to glabrous, crowned by persistent calyx and sometimes also the expanded disc, the calyx lobes 1.5—9 × 0.3—1 mm, reflexed or not, sericeous, the disc base to 0.3 mm high; pyrenes 4—5 (—6); seeds cylindric, laterally compressed, to 6 × 1 mm, pale brown.

TYPIFICATION: The type of *Guettardella ovatifolia* is *Brass 18667* ♀ (L holotype, n.v.; isotypes at A!, CANB!), collected at Newcastle Bay, 2.5 mi. S of Somerst, N Queensland, 7 May 1948.

DISTRIBUTION: Cape York Peninsula of Queensland, Australia.

ECOLOGY AND FIELD NOTES: Common in savanna forests, coastal scrub, or evergreen notophyll vine-forests, mainly growing on sand at elevations from 30 to 60 meters. The flowers [immature ?] are reported as green, the fruits as depressed-globose, black, fleshy, and palatable. Flowering and fruiting April to July and perhaps also earlier.

VERNACULAR NAMES: "Yoko" and "Lunisan" (New Castle Bay).

ADDITIONAL COLLECTIONS: **Australia.** QUEENSLAND: Somerst, *Bailey* s.n. (BRI); Lake Boronto - New Castle Bay, *Tracey 14333* (BRI); New Castle Bay, 2.5 km S of Somerst *Brass 18682* ♀ (A, CANB); Lockerbie, 10 mi. WSW of Somerst, *Brass 18547* ♀ (A, CANB, G); Mapoon, *Bailey* s.n. ♂ (BRI); Brown's Creek, Pascoe River, *Brass 19599* ♂ (A, CANB, G, SING); Lakefield, *Gasten 617* (BRI).

Although the young stipule bases of *Antirhea ovatifolia* are somewhat united, they differ from those of *A. buruana* and *A. hexasperma*, which are not early ruptured and separated by the developing shoot. Among the Australian taxa, *Antirhea ovatifolia* is ususual for its ovate leaves and a preference for sandy habitats.

27. **Antirhea paxillata** Chaw, sp. nov. FIGURES 8a, 12a

A speciebus nobis notis bene distincta, differt foliis lanceolatis et indumento nervos laminae paginae abaxialis restricto et reti venularum reticuli-paxillata.

Habit unknown; branchlets to 1.5 mm broad toward apex, slender, compressed, hirtellous, becoming terete, glabrous and glossy, dark purple-brown, the pale lenticels conspicuous; stipules imbricate, keeled, subcoriaceous, deltoid, to 7 × 2.5 mm, abruptly aristate (the arista shorter than or equaling stipule blade), hirsute outside, inside pale-sericeous and with colleters on lower half; petioles semiterete to nearly terete at base, 5—8 mm long, to 1 mm broad, hirsute; leaf blades narrowly ovate to lanceolate, thin-chartaceous, pale green when dried, 4—6 × 1.5—2 cm, gradually acuminate at apex, somewhat obtuse to rounded at base, sparsely hirtellous above (the hairs denser on costa), appressed-hirtellous to sericeous over venation beneath, the indument glossy and brownish yellow, the costa subplane to raised near apex above, elevated beneath, the secondary veins slender, subplane above, raised beneath, 6—7 on each side of costa, the intersecondary veins prominent beneath, the veinlets hardly distinguishable above, forming a striate pattern of areoles beneath, these arranged in parallel groups oriented perpendicular to secondary and intersecondary veins; domatia of tufted hairs in axils of secondary and intersecondary veins; ♂ inflorescences dichotomous, 3- to 6-flowered, at anthesis ca. 1 × 1.5 cm, the flowers often sessile and secund on inflorescence arms; peduncles slender, minutely sericeous, to 18 mm long, 0.8 mm broad; bracts narrowly deltoid to linear, acute at apex, 3—5 × ca. 0.4 mm, sparsely hirtellous on both surfaces, persistent; calyx tube to 0.4 mm long, puberulent at base within, the lobes 4, unequal, subcoriaceous, oblong-deltoid, 1.2—2.7 mm long, 0.4—0.8 mm broad at base, acute at apex, hirtellous over midrib outside, inside glabrous to sparsely hirtellous at apex; corolla narrowly salverform, the tube to 8 mm long, ca. 1 mm diam. at middle, densely sericeous outside, scattered-sericeous inside, the lobes 4, ovate, ca. 0.8 × 0.8 mm, obtuse at apex, sericeous to scabrous near margin; stamens 4, inserted ca. 0.5 mm below corolla throat, the anthers sessile, linear, ca. 2 × 0.3 mm, their tips exserted; abortive ovary obovoid, to 0.8 × 1 mm, hirtellous, 2-loculed, the disc 0.25 mm high, tomentose, the style cylindric, ca. 1.4 mm long, to 0.2 mm diam., papillose, bifid at apex, the slender branches included, to 0.4 mm long, scabrous; ♀ flowers and fruits not seen.

TYPIFICATION: The type of *Antirhea paxillata* is *BS 79440* (*Edano*) ♂ (A! holotype; isotype at BO!), collected on Mt. Babatgin, Cagayan Province, Luzon, Philippines, May 1930.

DISTRIBUTION: Presently known only from the type locality.

ECOLOGY AND FIELD NOTES: Unfortunately, no information as to habit or habitat is available.

Antirhea paxillata is unique among Old World *Antirhea* species in having lanceolate leaf blades with yellowish indument restricted to the abaxial venation. Reticuli-paxillate venation is well developed, the groups of parallel veinlets oriented perpendicular to the intersecondary and secondary veins.

28. **Antirhea philippinensis** (Benth.) Rolfe in J. Linn. Soc. Bot. 21: 312. 1884; Vidal, Phan. Cumig. Philipp. 119. 1885, Rev. Pl. Vasc. Filip. 154. 1886; Elmer in Leafl. Philipp. Bot. 3: 1009. 1911, op. cit. 4: 1329. 1912; Valeton in H. Hallier in Beih. Bot. Centralbl. 34(2): 44. 1916; non Elmer, 1912.

Guettardella philippinensis Benth. in Hooker's J. Bot. Kew Gard. Misc. 4: 197. 1852.
Antirhea microphylla sensu Merr. Enum. Philipp. Fl. Pl. 3: 540, *pro parte*. 1923; non sensu typi.
Guettardella microphylla sensu Jansen in Blumea 29: 577, *pro parte*. 1984; non sensu typi.

Shrub (?); branchlets to 1.5 mm broad toward apex, compressed, tomentose and with scattered, longer hairs, brownish, becoming terete, glabrous, and black-brown, the pale lenticels conspicuous; stipules valvate, somewhat keeled, chartaceous, lanceolate, 2.5—4 × 1—2 mm, abruptly and sharply acuminate, densely sericeous outside, inside minutely puberulent to densely sericeous toward base; petioles slender, semiterete, 1.5—2.5 mm long, ca. 0.3 mm broad, indument as on branchlets but shorter inside; leaf blades elliptic, chartaceous, 2—5 × 0.7—2 cm, acuminate at apex, acute to obtuse at base, sparsely and minutely puberulent above, scattered- and appressed-sericeous beneath (the hairs longer and denser over costa and secondary veins), the costa subplane to plane distally above, elevated beneath, the secondary veins slender, subplane above, raised beneath, ca. 5 on each side of costa, the veinlets hardly distinguishable above, forming elongate areoles beneath; domatia absent; ♂ inflorescences once to twice dichotomous, 3- to 7-flowered, at anthesis to 1 × 1.5 cm, the flowers often sessile and secund on the branching arms; peduncles slender, minutely sericeous, to 15 mm long, ca. 0.4 mm broad; bracts narrowly linear to acicular, acute at apex, 0.8—2 × ca. 0.3 mm, minutely puberulent on both surfaces, persistent; calyx tube to 0.4 mm high, sparsely puberulent at base within, the lobes 4, unequal, chartaceous, oblong-deltoid to linear, 0.8—1.5 mm long, 0.2—0.7 mm broad at base, acute to obtuse at apex, sparsely puberulent to glabrous beneath, glabrous above; corolla narrowly salverform, the tube ca. 5 mm long, 0.5 mm diam. at middle, densely appressed-puberulent outside, inside glabrous to villous near base, the lobes 4, ovate, ca. 1 × 0.8 mm, acute at apex, sericeous to scabrous at margin outside; stamens 4, inserted ca. 1 mm below corolla throat, the anthers sessile, linear, ca. 1.6 × 0.3 mm, their tips exserted; abortive ovary obovoid, to 0.5 × 0.5 mm, minutely puberulent, 2-loculed, the disc 0.2 mm high, puberulent, the style cylindric, to 1.2 mm long, ca. 0.1 mm diam., glabrous, bifid at apex, the slender branches included, to 0.4 mm long, glabrous; ♀ flowers and fruits not seen.

TYPIFICATION: *Guettardella philippinensis* is typified by *Cuming 1827* ♂, the holotype deposited at K (n.v.). Two isotypes at G(!) do not specify a locality, but Vidal (loc. cit.) reported that Cuming's collection was from Bohol Island, Philippines.

DISTRIBUTION: Presently known only from the type locality.

ECOLOGY AND FIELD NOTES: Unfortunately no information as to habit or habitat is available.

The present species was considered conspecific with *Antirhea microphylla* by Merrill and by Jansen, but in *A. philippinensis* the stipules are longer and have a more abruptly and sharply acuminate apex; the leaves have usually elliptic blades (versus usually ovate-lanceolate) and longer petioles; and the calyx lobes as well as corolla tubes are more slender.

29. **Antirhea putaminosa** (F. v. Muell.) Bailey Queensl. Fl. 3: 760. 1900; Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 8. 1909; C. T. White in J. Arnold Arbor. 27: 121. 1946. FIGURE 12b-c

Timonius putaminosus F. v. Muell. Fragm. 4: 92. 1864.
Bobea putaminosa F. v. Muell. Fragm. 4: 92. 1864, ibid. 5: 212. 1866; pro syn.
Guettardella putaminosa (F. v. Mueller) Benth. Fl. Austral. 3: 419. 1867; Jansen in Blumea 29: 584. 1984.
Guettarda putaminosa (F. v. Muell.) F. v. Muell. Fragm. 9: 183. 1875, Syst. Census Austral. Pl. 75. 1882.

Shrub or small tree to 5 m tall; branchlets ca. 1 mm broad toward apex, compressed and pubescent, becoming terete and glabrous; leaf scars raised; stipules valvate to slightly imbricate, subcoriaceous, deltoid to lanceolate, acute to acuminate at apex, to 2 × 1 mm, appressed-pubescent outside, densely sericeous inside and with scattered colleters except near apex; petioles slender, semiterete, to 3 mm long, ca. 0.5 mm broad, puberulent; leaf blades elliptic to obovate, coriaceous, 1.5—4 × 0.8—2.2 cm, usually emarginate to retuse and mucronulate (occasionally obtuse to subacute) at apex, at base acute to attenuate, somewhat revolute at margin, subglabrous above except near base and on costa, scattered-puberulent beneath (particularly over costa and secondary veins), the costa subplane above, prominulous to subplane near apex beneath, the secondary veins subplane on both surfaces, 3—4 on each side of costa, the veinlets hardly distinguishable; domatia absent; ♂ inflorescences simple to compound dichasia, occasionally thyrsoid, (1-) 3- to 25-flowered, at anthesis 0.5—1 × 1—2 cm, the flowers with pedicels to 2.5 mm long, or sometimes sessile and secund; peduncles slender, to 15 mm long, ca. 0.5 mm broad, sparsely puberulent to nearly glabrous; bracts acicular, to 0.8 × 0.2 mm, persistent; calyx tube ca. 0.6 mm high, inside pubescent at base, the lobes 4 (or sometimes the tube subtruncate to erose or undulate), deltoid, 0.2—0.6 mm long, 0.4—0.6 mm broad at base, acute to obtuse at apex, entire to ciliate at margin, sparsely puberulent outside, inside glabrous; corolla salverform, the tube to 3.5 mm long, ca. 1 mm diam. at middle, densely appressed-puberulent outside, scattered-sericeous basally inside, the limb ca. 2.5 mm broad, the lobes 4, ovate to rounded, to 1.2 × 1.2 mm, obtuse, pubescent outside; stamens 4, inserted ca. 1 mm below corolla throat, the anthers sessile, linear, to 2 × 0.4 mm, their tips subexserted; abortive ovary to 0.5 mm long, the style linear, ca. 2.5 × 0.3 mm, scabrous, bifid at apex, the slender branches included, unequal, to 0.5 mm long; disc 0.1 mm high, glabrous; ♀ flowers solitary; peduncles slender, to 20 mm long, ca. 0.3 mm broad; calyces similar to those of ♂

flowers; corolla narrowly infundibular, the tube to 2.5 mm long, ca. 1 mm diam. at middle, the limb ca. 2.5 mm broad, the indument similar to that of ♂ flowers; staminodia 4, linear, ca. 1.5 × 0.3 mm, sessile, included; disc 0.2 mm high, glabrous; style to 3 mm long, glabrous to slightly pubescent at middle, (4-) 5-(7-)branched, the branches subexserted, acicular, to 0.8 mm long; fruits ellipsoid to ovoid to subglobose, 4—7 mm long, 2.5—4 mm diam., glabrous, slightly ribbed or not, crowned by persistent calyx; pyrenes 4 or 5 or perhaps as many as 7, cylindric and laterally compressed, brown, to 4 × 0.7 mm.

TYPIFICATION: The type of *Timonius putaminosus* is mentioned by von Mueller as a *Thozet* collection (holotype in MEL, n.v.) from Rockhampton, Queensland; we have examined isotypes (♀) from A, BO, and K, all labeled in von Mueller's hand. In discussing *Guettarda putaminosa*, von Mueller erroneously credited the combination *Antirhea putaminosa* to J. D. Hooker (in Gen. Pl. 2: 100. 1873).

DISTRIBUTION: Queensland, Australia.

ECOLOGY AND FIELD NOTES: Frequently in dry creeks and dry scrub, or deciduous woods, semi-evergreen vine-thickets, mixed softwood scrub edges, and eucalypt forests on loamy soil. The outer bark is reported as flaky, the inner bark as pale brown or yellow-brown, and the fruits as black when ripe. Flowering probably between December and March, fruiting from March to July.

ADDITIONAL COLLECTIONS: **Australia.** QUEENSLAND: Barrabas, *Hyland 6066* ♀ (A, BRI); 38 mi. W of Nebo, *Story & Yapp 96* ♀ (CANB); 23 km SSW of Nebo, Dipperu National Park 72, Cockonize Parish, *Stanton 7* (BRI); Ogmore, *Johnson 1740* (BRI, CANB); W of Ogmore, *L. S. Smith 4759* ♀ (BRI); Stockyard Creek, 60 mi. N of Marlborough, *Jones 2809* (CANB); Marlborough, *Jones 1556* (CANB), *Jones 3004* ♀ (CANB), *Jones 3602* (CANB); Creek S of Marlborough, *Jones 1461* ♀ (CANB); Marlborough, Mt. Big Nose, *Jones 3063* (CANB); Marlborough, Sarina Road, *Jones 3180* ♀ (CANB); S Yaamba, ca. 20 mi. NW of Rockhampton, *Simmonds* s.n. ♀ (A, BRI); 14.4 mi. N of Rockhampton, *Speck 1694* (BRI, CANB); Milman via Rockhampton, *Webb 5136* ♀ (CANB); Etna Creek Lane near Rockhampton, *Webb 429* ♂ (BRI); Rockhampton, *Barnard* s.n ♀ (CANB), *Edger 244* ♀ (BRI); Neerkol Creek, *F. v. Mueller* s.n. ♂ (BO, G); Woodend, near Rockhampton, *Francis* s.n. ♀ (A, BRI).

Antirhea putaminosa is unusual in having emarginate to retuse and mucronulate leaf apices. In this species the branching patterns of staminate inflorescences are remarkably diverse, even in the same collection.

30. **Antirhea ramosii** Chaw, sp. nov. FIGURE 18

Antirhea microphylla sensu Merr. Enum. Philipp. Fl. Pl. 3: 540, *pro parte*. 1923.

Inter species *Antirhearum* Philippinarum lobis calycis brevi-oblongis et obtusis, ovariis oblongis et appressi-pubescentibus differt.

Habit unknown; branchlets 1.5 mm broad toward apex, compressed and brown-sericeous to somewhat spreading-hirtellous, becoming terete and glabrous, gray-brown; stipules imbricate, keeled, subcoriaceous, broadly triangular, sharply acuminate to abruptly aristate at apex, 3.5—8 × 2.5—4.5 mm, tomentose to somewhat hirtellous outside, inside pale-sericeous but glabrous toward margin, with scattered colleters on lower portion; petioles slender, to 25 mm long, ca. 1 mm broad, adaxially canaliculate, subterete at very base, tomentose to sericeous; leaf blades broadly elliptic to slightly ovate, chartaceous, (6—) 8—15 × 4—6

Figure 18. *Antirhea ramosii* (a–d from *BS 46597(Ramos & Edano)* ♀; e–f from *BS 18495* ♀). a. Habit, × 0.5. b. Adaxial surface of stipule, × 5. c. ♀ flower with 2 bracts, × 2.5. d. Style of ♀ flower, × 5. e. Fruit with 2 persistent bracts and portion of pedicel, × 2.5. f. Cross section of fruit, × 2.5.

(—8) cm, gradually acuminate at apex, at base acute to rounded, scattered-puberulent above (hirtellous over costa and lateral nerves), somewhat spreading-sericeous beneath (particularly over venation), the costa canaliculate, becoming distally prominulous above, elevated beneath, the secondary veins plane to prominulous above, raised beneath, 7—8 on each side of costa, the veinlets forming rectangular areoles but not in distinct groups; domatia obscure, of tufted hairs in axils of lateral veins; ♂ flowers not seen; ♀ inflorescences (1-) 3- or 4-flowered, dichotomous, at anthesis probably to 1.5 × 1 cm; peduncles to 25 mm long, ca. 5 mm broad, spreading-sericeous with yellowish indument; bracts linear, 4—6 × 0.4 mm, sparsely sericeous, persistent; calyx tube ca. 1.3 mm high, the lobes 4, oblong, the opposite pairs sometimes unequal in length, 0.3—1 mm long, 0.4—1 mm broad at base, obtuse at apex, outside densely sericeous, inside sparsely puberulent; corolla salverform, the tube to 4.5 mm long, ca. 1.5 mm diam. at middle, appressed-tomentose outside, inside scattered-puberulent at middle, the limb ca. 3 mm broad, the lobes 4, short-oblong, rounded at apex, ca. 1.2 × 1 mm, tomentose but often scabrous toward margin without; staminodia 4, inserted ca. 1 mm below corolla throat, the anthers sessile, linear, ca. 1.6 ×

0.2 mm; ovary distinctly oblong, densely sericeous with yellowish indument, 4-loculed, the disc sericeous, to 0.3 mm high, pubescent, the style linear, ca. 4 mm long, ca. 0.3 mm diam., glabrous, 4-branched, the slender branches to 1 mm long, subexserted, glabrous; fruits obovoid, appressed-pubescent, 4-ribbed, truncate at apex, acute at base, 8—10 mm long, 4—5 mm diam., crowned by persistent calyx, the exocarp fleshy, thin; pyrenes 4; seeds cylindric, pale brown, to 7 × 1 mm.

TYPIFICATION: The type of *Antirhea ramosii* is *BS 46597* (*Ramos & Edano*) ♀ (SING! holotype; isotypes at B!, NY!), collected from Peñablanca, Cagayan Province, Philippines, April 1926.

DISTRIBUTION: Cagayan and Isabella Provinces of Luzon, Philippines.

ECOLOGY AND FIELD NOTES: Flowering or fruiting pistillate specimens have been collected in March and April. No further information as to habit or habitat is available.

ADDITIONAL COLLECTIONS: **Philippines.** Cagayan, without further locality, *BS 18495* ♀ (US), *FB 17241* ♀ (US). Isabella, San Marinano, *Clemens 16835* ♀ (A, NY, US).

Among the Philippine taxa of *Antirhea*, the present species is recognized by its short-oblong and obtuse calyx lobes, as well as the oblong and appressed-pubescent ovary. Its relationship may be with *A. tayabensis*, but in that species the golden-brown indument is generally more dispersed, and the hairs coarser and longer; the calyx lobes are acute to acuminate and longer; and the domatia are in axils of both secondary and tertiary veins. The specimen *FB 17241*, cited above, was assigned by Merrill to *Antirhea microphylla*, but is clearly referable to the present species.

31. **Antirhea rhamnoides** (Baill.) Chaw, comb. nov. FIGURES 8b, 12d-e

Guettarda rhamnoides Baill. in Adansonia 12: 241. 1879; Guillaumin in Notul. Syst. (Paris) 1: 195. 1912, in Arch. Bot. (Paris) 3(5): 17. 1929, in Bull. Mus. Hist. Nat. (Paris) II. 1: 122. 1929, in op. cit. II. 6: 456. 1934, Fl. Nouv. Calédon. 331. 1948.

Shrub to tree 11 m tall; branchlets 1.5—2 mm broad toward apex, compressed, tomentose to nearly glabrous, brown, becoming terete, sparsely pubescent to glabrous and dark brown to black; stipules valvate, subcoriaceous, narrowly lanceolate, gradually acuminate, 4—7 × 2—3 mm, puberulent to glabrous outside, sericeous inside and with scattered colleters on lower half, the pale lenticels conspicuous; petioles semiterete, 10—20 mm long, to 2 mm broad, pubescent, the indument somewhat scattered and spreading abaxially; leaf blades elliptic to ovate to rarely obovate, chartaceous to subcoriaceous, 7—12.5 × 3—5.5 cm, gradually to abruptly acuminate at apex, acute to obtuse to sometimes rounded at base, sparsely appressed-pubescent above, scattered-sericeous to densely puberulent beneath (the hairs denser over venation), the costa subplane to plane above, raised beneath, the secondary veins plane to slightly prominulous above, elevated beneath, 3—6 on each side of costa, the veinlets striate and forming elongate areoles arranged in reticulate groups; domatia of tufted hairs in axils of lateral veins; ♂ cymes 3-flowered, at anthesis to 1 × 1 cm, the central flower

sessile, the lateral flowers subtended by 1 or rarely 2 bracts; peduncles to 20 mm long, 1 mm broad, scattered-pubescent to tomentose; bracts narrowly lanceolate to linear, 3.5—5 × 0.4—0.7 mm, acute, pubescent on both surfaces; calyx tube ca. 2 mm high, pubescent inside and out, the lobes 4, deltoid, sometimes slightly unequal, obtuse at apex, ca. 0.5 mm long, 1.4 mm broad at base, appressed-pubescent outside, sparsely pubescent inside; corolla salverform, the tube 5.5—7.5 mm long, ca. 1.5 mm diam. at middle, appressed-pubescent outside, sericeous on lower half inside, the limb to 5.5 mm wide, the lobes 4, ovate, ca. 2 × 1.5 mm; stamens 4, inserted ca. 1 mm below corolla throat, the anthers sessile, 3 × 0.5 mm, their tips exserted; abortive ovary ca. 0.5 mm long, the disc ca. 0.2 mm high, pubescent distally, the style ca. 3 mm long, 0.4 mm diam., minutely papillose, deeply bifid at apex, the slender branches included, ca. 1.7 mm long; ♀ flowers not seen; fruits solitary, subtended by 2 persistent bracts, obovoid to rhomboid, 4- or 5-ribbed, truncate at apex and sometimes also briefly constricted toward the persistent calyx, at base obtuse, 8—11 mm long, ca. 7 mm diam., appressed-puberulent, the calyx to 3 mm long; seeds 4—5.

TYPIFICATION: *Guettarda rhamnoides* was based on two collections, *Balansa 1128* (P, n.v.), collected at Daaoui de Cro, and *Balansa 1976* (P, n.v.) gathered near Kougni. Neither collection was included among loans requested for the present study, and, as far as we are able to determine, a lectotype has not been proposed.

DISTRIBUTION: New Caledonia.

ECOLOGY AND FIELD NOTES: Unfortunately, habit, habitat, and collection dates are unrecorded or undetailed for the collections examined; some collections were made in coastal forests or in wet forest above 400 m elevation. Flowering staminate specimens have been collected in January; fruiting specimens were gathered in June.

ADDITIONAL COLLECTIONS: **New Caledonia.** YATÉ: Port Boisy, ca. 20 km S of Yaté, *McPherson 2791* ♀ (MO); Wisseau, *Franc 2448* ♀ (A); *Vieillard 683* ♀ (A). New Caledonia, without further locality, *Balansa 344* ♀ (A), *Baumann-Bodenheim 14480* (Z); *Prony 1950* ♂ (A).

Indument is highly variable among the examined collections; McPherson's specimen is the least pubescent, Balansa's is heavily pubescent, and other collections are intermediate. The branchlets of *Baumann-Bodenheim 14480* are particularly slender with relatively long internodes and spreading indument.

32. **Antirhea sphaerocarpa** Chaw, sp. nov. FIGURE 19a-c

Species a congeneris fructibus parvis globosis, foliis parvis ellipticis, extremis nervorum secundariorum apices foliorum versus differt.

Shrub to 3 m tall; branchlets ca. 1 mm broad toward apex, compressed, pubescent, brown, becoming terete, glabrous, and gray-yellow; stipules slightly imbricate, deltoid to ovate, abruptly acuminate to somewhat mucronate at apex, keeled, 2.5—3.5 × 2 mm, outside hirsute over keel to dispersed-puberulent to glabrous toward margin, inside yellowish-sericeous and with colleters over lower portion; petiole slender, semi- to subterete at base, 3—5 mm long, to 0.8 mm

broad, somewhat appressed-hirtellous; leaf blades elliptic, chartaceous, 2—4.5 × 0.7—1.8 cm, gradually acuminate at apex, acute to nearly obtuse at base, appressed- and scattered-sericeous on both surfaces (the indument denser over costa and lateral veins), the costa canaliculate at base to plane near apex above, raised beneath, the secondary veins subplane above, prominent beneath, distally directed toward apex, 3—4 on each side of costa, the veinlets subplane beneath and mostly forming rectangular areoles; domatia in axils of lateral, intersecondary, and occasionally also tertiary veins, resembling small pits covered with tufted hairs; ♂ flowers not seen; ♀ flowers solitary; peduncles slender, to 15 mm long, ca. 0.2 mm broad, sparsely puberulent; bracts linear-acicular, 1.4—2 × 0.2 mm, pubescent, persistent; calyx tube ca. 0.4 mm high, the lobes 4, deltoid, ca. 0.3 mm long, 0.4 mm broad at base, sparsely sericeous to nearly glabrous outside, glabrous within; corollas not seen; ovary oblong-ovoid, yellowish-tomentose outside, 3- to 4-loculed, the disc ca. 0.2 mm high, distally puberulent; fruits with thin, fleshy exocarp, appressed-puberulent, black when dry, globose, ca. 3 mm diam., crowned by persistent calyx; seeds 3—4, cylindric, acute at apex, ca. 1.5 × 0.5 mm, brown.

TYPIFICATION: The type of *Antirhea sphaerocarpa* is *Docters van Leeuwen 10353* ♀ (A! holotype; isotypes at B!, K!), collected along the Rouffaer River, Djajapura Province, West New Guinea, September 1926.

DISTRIBUTION: Presently known only from the type locality.

ECOLOGY AND FIELD NOTES: Flowers (immature?) are recorded as greenish.

Antirhea sphaerocarpa is unusual in its small, globose fruits. The small, elliptic leaf blades with relatively few secondary veins directed apically are readily distinguishable from those of other Malesian *Antirhea* species.

33. **Antirhea talaudensis** Chaw, sp. nov. FIGURE 19d-j

Guettardella microphylla sensu Jansen in Blumea 29: 577, *pro parte*. 1984; non sensu typi.

Species a congeneris foliis basi cordatis usque rotundatis, ovariorum loculis et stylorum ramis in floribus pistillatis et staminatis aequinumerosis differt.

Shrub (?); branchlets ca. 1.5 mm broad toward apex, compressed (or sometimes trigonal), densely puberulent to tomentose and sometimes also with longer, scattered indument, becoming terete and glabrous, gray- to purple-brown, the lenticels pale, the leaf scars distinctly raised; stipules valvate, subcoriaceous, somewhat keeled, lanceolate, 5—8 × 1.5—2.5 mm, gradually to abruptly acuminate, pubescent to sericeous outside, inside densely pale-sericeous and with colleters scattered near base; petioles slender, to 3 mm long, ca. 1 mm broad, tomentose and scattered-hirtellous (especially abaxially); leaves aggregated toward tips of branchlets, usually opposite, sometimes in whorls of 3, the blades usually ovate to broadly lanceolate, chartaceous, 3—5.5 × 1.5—3 cm, acuminate at apex, at base cordate to rounded, glabrous above except over costa and sometimes secondary veins, appressed-sericeous over venation beneath (but hirtellous on costa), the costa and secondary veins subplane to prominulous above, raised beneath,

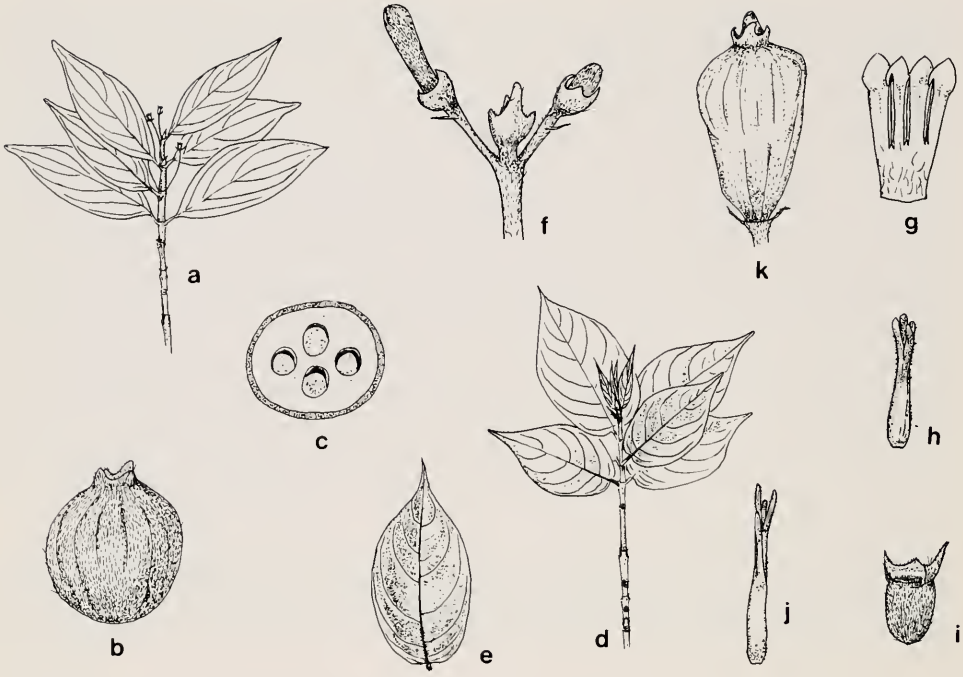


Figure 19. a—c. *Antirhea sphaerocarpa* (*Docters van Leeuwen 10353* ♀). a. Habit, × 0.5. b. Fruit, × 5. c. Cross section of fruit showing 4 seeds, × 5. d—k. *A. talaudensis* (*Lam 3260* ♂ & ♀). d. Habit, × 0.5. e. Adaxial surface of leaf blade, showing cordate base, × 0.5. f. Simple dichasium showing 2 lateral ♂ flower buds and 1 terminal flower after anthesis, × 5. g. Adaxial surface of ♀ corolla with 1 staminodium removed. h. Style of ♀ flower. i. Ovary and persistent calyx (with 1 calyx lobe removed) showing pubescent disc. j. Style of ♂ flower, × 10. k. Fruit and portion of peduncle with persistent bracts, × 2.5.

the secondary veins 5 on each side of costa, the veinlets hardly distinguishable above, distinct beneath and forming elongate areoles; domatia obscure, of tufted hairs in axils of secondary veins; ♂ inflorescences (immature) simple dichasia, 3-flowered, at anthesis probably to 0.5 × 0.6 cm; peduncles slender, to 10 mm long, ca. 0.3 mm broad, scattered-pubescent; bracts linear to bristle-like, to 2 × 0.3 mm, acuminate, pubescent, persistent; calyx tube to 0.4 mm high, the lobes 4, oblong-deltoid to oblong, 0.3—0.6 mm long, to 0.5 mm broad at base, the opposite pairs differing in shape and length, obtuse at apex, sparsely pubescent; corolla (immature) salverform, the tube ca. 2.6 mm long, 1 mm diam. at middle, appressed-pubescent outside, inside scattered-sericeous over lower half, the limb ca. 2.5 mm broad, the lobes 4, broadly ovate, 0.7 × 0.7 mm, obtuse at apex; stamens 4, inserted ca. 0.5 mm below corolla throat, sessile, the anthers linear, to 1.8 × 0.2 mm; abortive ovary ca. 0.5 mm long, scattered-pubescent, 4-loculed, the disc 0.1 mm high, pubescent, the style filiform, ca. 1.4 mm long, 0.2 mm diam., glabrous, 4-branched at apex, the slender branches included, unequal, glabrous; ♀ flowers solitary; peduncles slender, to 20 mm long, ca. 0.3 mm broad, pubescent; bracts and calyces resembling those of ♂ flowers; corolla (immature) infundibular, the tube ca. 1.5 mm long, to 1 mm diam. at middle,

appressed-pubescent outside, inside glabrous; staminodia 4, sessile, linear, ca. 1.1 × 0.3 mm; ovary to 2 mm long, 1 mm diam., appressed-pubescent, 4-loculed, the disc 0.2 mm high, pubescent, the style (immature) tetragonal, ca. 1.2 mm long, to 0.3 mm diam., scattered-papillose, 4-branched, the slender branches probably subexserted, to 0.4 mm long; fruits dispersed-puberulent, obovoid, ca. 8 mm long, 4 mm diam., crowned by persistent calyx; pyrenes probably 4.

TYPIFICATION: This new species is typified by *Lam 3260* p.p. ♀ (BO! holotype; isotype at SING!), collected on E slope of G. Piapi, Karakelang, Talaud Island, 31 May 1926. The type collection includes only pistillate specimens; a staminate specimen bearing the same number is at A(!).

DISTRIBUTION: Presently known only from Talaud Island, Indonesia.

ECOLOGY AND FIELD NOTES: The one available collection bears the notation "open and sunny slope, common, scattered, 3 m high, calyx dirty red."

VERNACULAR NAME: "Omin'a."

Antirhea talaudensis is characterized by leaf blades that are usually cordate to rounded at base. The species is also unusual in that the number of ovary locules and style branches is the same in both staminate and pistillate flowers, at least in the very limited material at hand.

34. **Antirhea tayabensis** Chaw, sp. nov. FIGURES 3a & d, 8c-d, 20

Antirhea livida sensu Merr. Enum. Philipp. Pl. 3: 540, *pro parte*. 1923; non sensu typi.
Guettardella livida sensu Jansen in Blumea 29: 576, *pro parte*. 1984; non sensu typi.

Ex affinitate *Antirhea livida* sed indumentis plerumque flavidis vel aureo-brunneis et aliquam hirsutis, foliis tenuioribus, fructibus comparate grandioribus et inflorescentiis extense ramosioribus differt.

Habit unknown; branchlets 1.5—2 mm broad toward apex, somewhat compressed, hirsute, yellow, becoming terete, pubescent to glabrous, gray-brown to dark purple; stipules imbricate, chartaceous to subcoriaceous, deltoid, slightly keeled, abruptly aristate, 4—7 × 3.5—5 mm, hirsute to sparsely puberulent at margin outside, sericeous to nearly glabrous at margin inside, and with colleters scattered centrally; petioles slender, semiterete to subterete, 11—20 mm long, 0.8—1.2 mm broad, hirsute; leaf blades elliptic to rarely ovate, thin-chartaceous to membranous, 7—12 × 3.5—6 cm, gradually to sometimes abruptly acuminate at apex, acute to nearly rounded at base, greenish to brownish yellow-hirsute on both surfaces (the hairs denser over costa and secondary veins), the costa canaliculate at base to prominulous toward apex above, raised beneath, the secondary veins subplane above, prominent beneath, spreading, 6—8 on each side of costa, the tertiary veins distinctly raised and percurrent to reticulate beneath, the veinlets striate and forming a reticulum of grouped, elongate areoles; domatia of tufted hairs in axils of secondary and tertiary veins; ♂ inflorescences compound dichasia, (5-) 8- to 14-flowered, at anthesis to 3.5 × 4 cm, the flowers with pedicels to 4 mm long or sessile and secund; peduncles slender, compressed, 3.5—6.5 mm long, ca. 0.8 mm broad, hirsute, golden-brown; bracts

Figure 20. *Antirhea tayabensis* (a, c–d from *BS 28869* (*Ramos & Edano*) ♀; b from *BS 45253* (*Ramos & Edano*) ♂; e–f from *BS 28982* (*Ramos & Edano*) ♀). a. Habit, × 0.5. b. Terminal flower and lateral branch of ♂ inflorescence, showing spreading trichomes × 2.5. c. ♀ flower, × 2.5. d. Style, × 2.5. e. Fruit with persistent calyx and bracts, × 2.5. f. Cross section of fruit showing 4 ribs and seed-locules, × 2.5.

linear to bristle-like, to 4.5 × 0.3 mm, acute, persistent; calyx tube to 0.8 mm high, the lobes 4 (occasionally 5), arranged as opposite pairs of different length, chartaceous, oblong-deltoid to narrowly oblanceolate, 0.6—5 mm long, 0.4—0.8 mm broad at base, acute at apex, hirsute outside, inside sparsely sericeous; corolla salverform, the tube to 9 mm long, 1.3 mm diam. at middle, appressed-tomentose outside, sparsely sericeous over lower half inside, the limb to 3.5 mm broad, the lobes 4, to 1.5 × 1 mm, rounded at apex; stamens 4, inserted ca. 1 mm below

corolla throat, the anthers subsessile, linear, ca. 3 × 0.3 mm, their tips exserted; abortive ovary to 0.8 mm long, 2-loculed, golden-brown hirsute, the disc 0.2 mm high, tomentose distally, the style linear, ca. 3 mm long, 0.3 mm diam., glabrous, bifid at apex, the slender branches included, ca. 2 mm long, glabrous; ♀ inflorescence usually once- to rarely twice-dichotomous, (1-) 2- or 3- (4-)flowered, at anthesis to 2 × 2 cm, the central flower sessile; peduncles slender, to 40 mm long, 1.5 mm broad, compressed distally, scattered-hirsute, yellowish; bracts, calyces, and corollas similar to those of ♂ flowers, but the corolla tube slightly shorter, 6—7 mm long, inside sparsely sericeous basally; staminodia 4, inserted ca. 0.5 mm below corolla throat, subsessile, linear, ca. 2 × 0.2 mm; ovary subovoid, ca. 2.5 mm long, 1 mm diam., 2- to 4-loculed, golden-brown hirsute, the disc ca. 0.25 mm high, tomentose distally, the style 4.5—7 mm long, ca. 0.5 mm diam., glabrous, (2-) 3- or 4-branched, the slender branches exserted, slightly unequal, linear, to 0.8 mm long, 0.3 mm broad, glabrous; fruits brown-hirsute, narrowly obovoid with 3—4 ribes, 9—12 mm long, ca. 5 mm diam., obtuse to rounded at both ends, crowned by persistent calyx (ca. 2—4 mm long), the exocarp fleshy, thin, dark purple; seeds 3—4 (probably sometimes 2), cylindric, laterally compressed at apex, 6—10 × 0.8 mm, pale brown.

TYPIFICATION: The type of *Antirhea tayabensis* is *BS 28869* (*Ramos & Edano*) ♀ (NY! holotype; isotypes at A!, BM!, BO!, P!, US!), collected on Mt. Binuang, Quezon ("Tayabas") Province, Luzon, May 1917.

DISTRIBUTION: Quezon Province, Luzon, Philippiues.

ECOLOGY AND FIELD NOTES: Flowering and fruiting specimens have been gathered from May to September.

ADDITIONAL COLLECTIONS: **Philippines.** NUEVA ECIJA: Mt. Umingan, *BS 26368* ♂ (A, BO, K, SING). QUEZON: Casiguran, *BS 45253* ♂ (B, BM, BO, NY, SING, US); Mt. Binuang, *BS 28514* (*Ramos & Edano*) ♂ (A, BM, BO, US); Umiray, *BS 28982* ♂ (A, BO, US).

Merrill assigned the examined specimens (except *BS 45253*) to *Antirhea livida*, and the species are closely related, but in *A. tayabensis* the indument is usually yellowish to golden brown and more coarsely hirsute, the leaves are thinner in texture with distinctly striate veinlets, and the fruits are larger; in addition, the more extensively branched inflorescences of *A. tayabensis* are quite distinct. The present species is also similar to *A. ramosii* (q.v.).

35. **Antirhea tenuiflora** F. v. Muell. ex Benth. Fl. Austral. 3: 418. 1867; F. v. Muell. Fragm. 7: 48. 1869; F. M. Bailey, Queensl. Fl. 3: 760. 1900; Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 8. 1909; C. T. White in J. Arnold Arbor. 27: 121. 1946; non Urban, Symb. Antill. 1: 438. 1899.

FIGURES 8e-f, 12l-m

Guettarda tenuiflora (F. v. Muell. ex Benth) F. v. Muell. Fragm. 9: 183. 1875, Syst. Census Austral. Pl. 75. 1882.
Guettardella tenuiflora (F. v. Muell. ex Benth.) Jansen in Blumea 29: 586. 1984.

Shrub or tree to 20 m tall; branchlets ca. 1.5 mm broad toward apex, compressed, tomentose, becoming terete, glabrous, gray-brown to dark brown; stipules

valvate, narrowly deltoid to lanceolate, acuminate, (2.5—) 4.5—9 (—11) × 1.5—2.5 mm, appressed-pubescent outside, densely sericeous inside with scattered colleters centrally; petioles semiterete, grooved adaxially, somewhat winged by leaf blade, (5—) 10—25 mm long, 0.8—1.5 mm broad, tomentose; leaf blades narrowly elliptic to elliptic, chartaceous to subcoriaceous, 6.5—15 (—19) × 2—6 cm, acute to abruptly acuminate at apex, at base acute to gradually acuminate, somewhat decurrent onto petiole, glossy and glabrous above, sparsely appressed-puberulent beneath (the hairs denser over costa and secondary veins), the costa slender, canaliculate above, raised beneath, the secondary veins canaliculate above, prominent beneath, 4—6 on each side of costa, the veinlets distinct beneath and forming a reticulum of grouped areoles; domatia of tufted hairs in axils of secondary and tertiary veins; ♂ inflorescences once- to twice-dichotomous, 15- to 20- (40-)flowered, at anthesis to 2 × 1.5 cm, the flowers often sessile and secund; peduncles 4—15 mm long, to 1 mm broad, appressed-tomentose; bracts lanceolate to narrowly deltoid to rarely scale-like, acute to acuminate, 0.3—1 × ca. 0.5 mm, pubescent on both surfaces, persistent; calyx tube, ca. 0.4 mm long, pubescent outside, inside pubescent basally, the lobes 4 or rarely 5, deltoid, pubescent outside, glabrous inside, the margin entire to ciliate; corolla salverform, (6—) 8—13 mm long, to 1 mm diam. at middle, pubescent outside, inside pubescent basally, the limb to 5.5 mm broad, the lobes 4, ovate, 1.4—2 × 1.2—1.5 mm, obtuse; stamens 4, inserted ca. 1.5 mm below corolla throat, the anthers sessile, linear, 3—4 × ca. 0.3 mm, their tips exserted; abortive ovary to 1.2 × 1 mm, pubescent, the disc ca. 0.1 mm high, glabrous, the style acicular, to 4 mm long, 0.3 mm diam., pubescent, bifid at apex, the slender branches included, to 0.8 mm long, glabrous; ♀ inflorescences simple to compound dichasia, (1-) 3- to 7-flowered, the flowers often sessile and secund on branching arms or with pedicels to 3 mm long; peduncles and calyces similar to those of ♂ plants; corolla narrowly infundibular, the tube to 6 mm long, ca. 0.8 mm diam. at middle, indument resembling that of ♂ flowers, the limb to 4.5 mm broad, the lobes 4, ovate, 0.8 × 0.6 mm; staminodia 4, the anthers sessile, ca. 1.7 × 0.3 mm, included; ovary pubescent, to 2.5 mm long, 1 mm diam., the style to 5.5 mm long, pubescent basally, usually 3-branched (or sometimes more?), the slender branches exserted, to 1 mm long, glabrous; fruits sparsely and minutely puberulent, pink to red, obovoid, regularly or sometimes irregularly 3- (5-)ribbed, sometimes laterally compressed, 10—15 mm long, 3.5—8 mm diam., obtuse to truncate at apex, acute at base, crowned by persistent calyx; seeds 2—4 (—5).

TYPIFICATION: *Antirhea tenuiflora* is based on a *J. Dallachy* collection gathered at Rockingham Bay, Queensland, Australia. A specimen at K(!), annotated with the species name and brief description in von Mueller's hand, is perhaps the holotype (isotypes at BO!, G!, GOET!). Bentham had mentioned no fruit being seen by him; the type collection bears staminate flowers only. Unattached fruits on specimens from BO and GOET may be accidentally associated.

DISTRIBUTION: Eastern Queensland, Australia, and extending to southern New Guinea.

ECOLOGY AND FIELD NOTES: Obviously confined to the understory of rain forests and vine-forest habitats ranging from ca. 15 to 900 m elevation (average

rainfall from 80 to 125 inches). The species occurs mainly on clays or coarse sandy clays derived from various rocks. The outer bark surface is recorded as brownish black, corky, and very finely pustular, the inner bark as pinkish to yellowish brown. The flowers are reported as pale greenish cream-colored, white, or rarely green, the mature fruits as red and fleshy with 3 or 4 ribs. Flowering and fruiting between July and March.

ADDITIONAL COLLECTIONS: **West New Guinea.** DIGUL: Along Digoel River, near Wage, *BW 4853* ♀ (CANB, L). **Papua New Guinea.** WESTERN: Tarara, Wassi Kussa River, *Brass 8525* ♂ (A, BM, BO, BRI), *8585* ♀ (A, BO, BRI). **Australia.** QUEENSLAND: Tozer Gap, Tozer Range, *Brass 19439* ♂ (A, BRI); Leo Creek, upper Nesbit River, *Brass 19861* ♀ (A, BRI, CANB, G); Headwaters of Lankelly Creek, *Webb & Tracey 9557* ♂ (BRI); Kamerunga, Barron River area, *Cowley 28B* (BRI), *Cowley 30C* (BRI); Bloomfield River area, 1 mi. NE of Stuckies Gap, *Webb & Tracey 8741* (BRI); 16°20′S, 145°19′E, *Irvine 922* ♀ (BRI), *Irvine 1708* ♀ (BRI); Tully Fall, *L. S. Smith 4749* ♂ & ♀ (A, CANB); S.F.R. 650 E/P 29, Mt. Fisher, *Sanderson 820* (CANB); 17°10′S, 145°35′E, *Risley 4* (BRI); 17°9′S, 145°38′E, *Sanderson 267* ♀ (CANB); Mossman, *Brass 2111* ♀ (A, BRI, NY), *L. S. Smith 3947* ♂ (A, BRI); Rumula, Rex Highway, *Mckee 9099* ♀ (BRI, CANB, P); Bailey's Creek, N of Daintree River, *Webb & Tracey 6509* (BRI); Daintree, *Brass 182* ♂ (BRI); Etty Bay, near Innisfail, *L. S. Smith 3251* ♂ (A, BRI); Davis Creek, Mareeba, *Jones 2309*, (CANB), *Jones 2430* ♀ (CANB), *Jones 2845* (CANB), *Jones 3570* (CANB), *L. S. Smith 5266* ♀ (A), *Webb & Tracey 7236* (BRI), *Webb & Tracey 11414* ♀ (CANB); Lock Creek, ca. 12 mi. along Davis Creek forestry road, *L. S. Smith 12078* ♀ (A), *L. S. Smith 12058* ♀ (BRI); Danbulla, *L. S. Smith 3760* ♂ & ♀ (A, BISH, CANB); Robson Ramp, *L. S. Smith 4179* (BRI); Smithfield near Kuranda, *Webb & Tracey 5951* ♀ (BRI, CANB); S.F.R. 700, Gilles L.A., ca. 8 km NE of Lake Barrine, *Moriarty 2014* ♀ (CANB); Bartle Frere, *Webb & Tracey 5801* ♀ (CANB); between El Arish and Mission Beach road, *Webb & Tracey 6745* (BRI); Mission Beach via Tully, *M. S. Clemens* s.n. ♀ (BRI); Yarrabah, *Michael 626* ♂ (BO, BRI), *Michael 1646* ♀ (BRI); Malbon-Thomson Range, *Jones 1316* ♀ (CANB); Mt. Fox, *M. S. Clemens* s.n. ♀ (BRI); Johnstone River, *Michael* s.n. ♂ (A); Lacey's Creek, Mission Beach, 6 km W of Clump Point, *Crome 39* ♀ (CANB); Dank Is., on hill behind Brammo Bay, *Webb & Tracey 10663* (BRI); Gregory Falls, *Webb & Tracey 6633* (BRI); Brandy Creek, Conway Range, *Byrnes & Clarkson 3586* (BRI); Ravenshoe District, without further locality: *Martin 16* ♀ (BRI). Queensland, Bamaga, *Jones 2561* ♂ (BRI); Boonjie, *Webb 1014* (BRI); Headwaters of Goanna Creek, *Webb 3120* (BRI); Gadgarra, *C. T. White 1576* ♀ (A, BRI).

Antirhea tenuiflora is remarkable for its short peduncles and usually obovoid, 3-ribbed fruits.

36. **Antirhea ternata** Chaw, sp. nov. FIGURE 15d-i

Species florum partibus cum *Antirhea bombysiis* optime congruens, sed differt foliis tenuioribus et grandioribus, forma domatiorum, et florum bractearum, et inflorescentiis multum ramosis.

Habit unknown; branchlets ca. 2 mm broad toward apex, compressed, tomentose and with scattered, longer hairs, becoming terete and glabrous, pale brown, the leaf scars raised, the lenticels obscure; stipules slightly imbricate (?), chartaceous, deltoid-lanceolate, 5—8 × 3 mm, abruptly and sharply acuminate, puberulent outside, inside densely sericeous and with centrally scattered colleters; petioles semiterete to subterete at base, ca. 10 mm long, 1.5 mm broad, the indument as on branchlets; leaf blades elliptic, thin-chartaceous to membranaceous, gradually acuminate at apex, at base usually obtuse to acute, 7.5—13 × 2.5—5 cm, spreading-pubescent above, the indument denser and subappressed beneath, the costa canaliculate to subplane distally above, raised beneath, the secondary veins subplane to prominulous above, raised beneath, 7—8 on each side of costa, the veinlets mostly arranged in groups and forming elongate areoles; domatia of tufted hairs in axils of secondary and tertiary veins; ♂ inflorescences

compound dichasia, 10- to 22-flowered, at anthesis ca. 2 × 3 cm, the flowers often sessile and secund, or with pedicels to 2 mm long; peduncles slender, to 35 mm long, 1 mm broad, spreading-pubescent; bracts linear, gradually acuminate, ca. 4 × 0.5 mm, pubescent, persistent; calyx tube ca. 1.5 mm high, scattered-sericeous outside, inside glabrous; calyx lobes usually 3 (one of them distinctly larger than the others), oblong-deltoid to narrowly deltoid, thin-chartaceous, 0.8—3 mm long, to 1 mm broad at base, acute to obtuse at apex; corolla salverform, the tube to 5.5 mm long, ca. 0.5 mm diam. at middle, densely sericeous outside, inside glabrous, the limb to 3 mm broad, the lobes 4, ovate, ca. 0.8 × 0.8 mm, obtuse; stamens 3, inserted ca. 0.5 mm below corolla throat, the anthers sessile, linear, ca. 1.6 × 0.2 mm, their tips exserted; abortive ovary obscure, ca. 0.4 × 1 mm, 2-loculed, the style included, filiform, to 3 mm long, ca. 0.1 mm diam., glabrous, bifid at apex, the slender branches unequal, to 0.6 mm long; ♀ flowers and fruits not seen.

TYPIFICATION: *Antirhea ternata* is typified by *BS 34916* (*Ramos & Pascasio*) ♂ (SING! holotype; isotypes at BO!, NY!), gathered on Siargo Island (without detailed locality), Philippines, June 1919.

DISTRIBUTION: Presently known only from the type collection.

Antirhea ternata and *A. bombysia* are the only *Antirhea* species with 3-merous perianths and androecia. However, in its thinner and larger leaf blades, domatia, flower bracts, and much-branched inflorescence, the present species is readily distinguishable. *Antirhea ternata* is similar to *A. tayabensis,* particularly to specimens from Nueva Ecija Province, but distinct in the number of floral parts, and the narrower leaf blades with shorter, more spreading indument on the adaxial surface.

EXCLUDED SPECIES

Antirhea borneensis Valeton in H. Hallier in Beih. Bot. Centralbl. 34(2): 43. 1916.
= *Timonius flavescens* (Jack) Baker, Fl. Maurit. 144. 1877; Merr. Enum. Born. Pl. 568. 1921; Jansen in Blumea 29: 587. 1984.

The syntypes of *Antirhea borneensis* are *Foxworthy 278* and *Hose 64* (specimens of the latter at K and L, fide Jansen); no material of the former collection was seen, and we are not aware of any lectotypification.

Antirhea esquirolii H. Lév. Fl. Kouy-Tchéou, 364. 1915.
= *Ecdysanthera rosea* Hook. & Arnott, Bot. Beechey Voy. 198, *tab. 42.* 1836; Rehder in J. Arnold Arbor. 18: 235. 1937; Lauener & Ferguson in Notes Roy. Bot. Gard. Edinb. 32: 103. 1972; Lauener in op. cit. 37: 131. 1978; Jansen in Blumea 29: 587. 1984. (Apocynaceae).

In describing *Antirhea esquirolii* Léveillé cited neither a specific collection nor locality. Rehder reported the type as *J. H. Esquirol 867* (photo and isotype in A, fide Rehder, 1937), collected from "Kouy-Tcheuo" (Guizhou), China, with further locality illegible; we have not examined the specimen.

Antirhea ? martini H. Lév. in Fedde Repert. 13: 178. 1914, Fl. Kouy-Tchéou. 364. 1915.

= *Sindechites henryi* Oliver in Hook. Icon. Pl. 18: *tab. 1772*. 1888; Rehder in J. Arnold Arbor. 18: 238. 1937; Fang, Icon. Pl. Omeiens. *tab. 87*. 1944; Lauener & Ferguson in Notes Roy. Bot. Gard. Edinb. 32: 103. 1972; Lauener in op. cit. 37: 131. 1978; Jansen in Blumea 29: 587. 1984. (Apocynaceae).

The syntypes of *Antirhea martini* are *L. Martin 2300* and *J. Cavalerie 1025* (photos of both in A, fide Rehder, 1937), collected from Gan-pin, Guizhou, 5 June 1898, and Pin-fa, Guizhou, 3 June 1903, respectively; we have not examined either collection.

Antirhea myrtoides (F. v. Muell.) Bailey, Queensl. Fl. 3: 760. 1900; C. T. White in J. Arnold Arbor. 27: 122. 1946. *Guettarda myrtoides* F. v. Muell. Fragm. 9: 184. 1875, Syst. Census Austral. Pl. 75. 1882.

= *Bobea myrtoides* (F. v. Muell.) Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 7. 1909; Jansen in Blumea 29: 587. 1984.

Guettarda myrtoides is typified by *J. Dallachy* s.n. (MEL holotype, n.v.; isotypes at A (photo!), BRI!, K!), gathered at Rockingham Bay, Queensland, 11 November 1870, the only collection cited by von Mueller. Judging from the photograph at A, the holotype includes both pistillate and staminate material. The specimen in BRI is accompanied by two envelopes on the same sheet; the one enclosing a staminate flower has the remark "one of the three flowers only on the type," while the other contains a nearly mature fruit. The specimen at K bears an attached, broken peduncle. The protologue mentions both staminate and pistillate structures.

The drupe with 4 free pyrenes was the basis of Valeton's generic determination, and we agree that on that basis alone the species cannot be accommodated in *Antirhea*, while the strongly imbricate corolla lobes and few pyrenes (as many as 4) do suggest a relationship with *Bobea*. Having examined some 20 additional collections (all from Queensland) of this taxon, we tentatively accept Valeton's generic placement. Superficially resembling *Antirhea tenuiflora* F. v. Muell. ex Benth. are yet other Queensland collections, again with free pyrenes and imbricate corolla lobes, that likewise may be assignable to *Bobea*. Further study is required before a firm conclusion can be reached as to whether or not *Bobea* should be expanded to incorporate taxa outside the Hawaiian Islands.

Guettardella sandwicensis (A. Gray) H. Mann in Proc. Amer. Acad. Arts 7: 170. 1867; Jansen in Blumea 29: 587. 1984. *Chomelia ? sandwicensis* A. Gray in Proc. Amer. Acad. Arts 4: 38. 1860.

= *Bobea sandwicensis* (A. Gray) Hillebr. Fl. Haw. Isl. 174. 1888; Darwin & Chaw in W. L. Wagner et al., Man. Fl. Pl. Hawai'i, 1117, *pl. 161*. 1990.

Chomelia sandwicensis is typified by a U. S. Exploring Expedition collection (probably at US and perhaps also at GH, n.v.) from Oahu, Hawaiian Islands. Hillebrand transferred Gray's species to *Bobea* on account of the drupes having

2 free pyrenes, and Jansen ascribed the taxon to *Guettardella* with some doubt. The species correctly belongs in the segregate genus *Bobea*, which is thus far know with certainty only from the Hawaiian Islands (Darwin & Chaw, 1990).

Insufficiently Known Species

Antirhea strigosa Korthals, Ned. Krudik. Arch. 2: 217. 1851; Valeton in Bull. Dép. Agric. Ind. Néerl. 26: 8. 1909, in H. Hallier in Beih. Bot. Centralbl. 34(2): 44. 1916; Jansen in Blumea 29: 587. 1984.

In proposing this species, Korthals did not cite a collection, giving only habitat and locality - "Crescit in sylvis humilioribus Doekoe, Padang, Sumatra." It is likely that *Antirhea strigosa* was based on Korthals's own collection, but Jansen states that no material referable to the species could be found at L. Since no other *Antirhea* specimen is available from Sumatra, the status of Korthals's species is still in doubt; Jansen suggested that it could be the "common Sumatran species" referred to but not named by J. D. Hooker (Fl. Brit. India 3: 126. 1880, footnote).

Acknowledgments

Sincere appreciation is expressed to the administrators of the following institutions who kindly made their herbarium collections available for study (herbarium abbreviations from Holmgren et al., 1990): A, B, BISH, BM, BO, BRI, CANB, E, G, GH, GOET, IBSC, K, L, LAE, MEL, MO, NO, NY, P, PH, PNH, PR, PRC, SING, U, US, W, WRSL, WU, Z. The preliminary accumulation of literature and travel to North American herbaria were supported by grants to S.-M. Chaw from the Society of the Sigma Xi (Tulane Chapter) and the Graduate School of Tulane University. The cost of supplies was partially underwritten by a grant from the National Science Foundation to S. P. Darwin, and by the Biology Department of Tulane University. We thank Professor and Mrs. Joseph Ewan for their valuable help with botanical literature; Mr. Wei-Chiu Chen, who reviewed portions of the manuscript; and Drs. David H. Lorence, Albert C. Smith, and Charlotte M. Taylor, who gave much useful advice.

Literature Cited

Airy Shaw, H. K. 1973. A Dictionary of the Flowering Plants and Ferns by J. C. Willis (ed. 8).

Baillon, H. E. 1880. Histoire des Plantes. Vol. 7. (Rubiaceae, pp. 257-503).

Balgooy, M. M. J. van. 1971. Plant-geography of the Pacific. Blumea Suppl. 6: 1-222.

Bakhuizen van den Brink, Jr., R. C. 1975. A synoptical key to the genera of the Rubiaceae of Thailand. Thai Forest Bull. (Botany) 9: 15-53.

Bentham, G. 1852. Flora Hongkongensis: an enumeration of plants collected in the island of Hong-Kong by Major J. G. Champion. Hooker's J. Bot. Kew Gard. Misc. 4: 193-199.

_____. 1867. Flora Australiensis. Vol. 3. (Rubiaceae, pp. 399-477).

Bremekamp, C. E. B. 1952. The African species of Oldenlandia L. sensu Hiern et K. Schumann. Verh. Kon. Akad. Wetensch., Afd. Natuurk., Tweede Sect. II. 48: 1-297.

_____. 1959. A species of Antirhea (Rubiaceae) from Suriname. Acta Bot. Neerl. 8: 479-481.

_____. 1966. Remarks on the position, the delimitation and the subdivision of the Rubiaceae. Acta Bot. Neerl. 15: 1-33.

Candolle, A. P. de. 1830. Prodromus Systematis Naturalis. Vol. 4. (Rubiaceae, pp. 341-622).

Darwin, S. P. 1980. Leaf-venation and the classification of certain Rubiaceae (Abstract). The University of British Columbia, Second International Congress of Systematic & Evolutionary Biology (p. 176).

_____. (in press). A revision of Timonius subgenus Timonius (Rubiaceae: Guettardeae). Allertonia.
DARWIN, S. P. & S.-M. CHAW. 1990. Bobea. *In:* W. L. Wagner, D. R. Herbst, & S. H. Sohmer, Manual of the Flowering Plants of Hawai'i (pp. 1114-1118).
DESROUSSEAUX, L. A. J. 1792. Antirhea. *In:* J. B. de Lamarck, Encyclopédie Méthodique 3: 688.
DWYER, J. D. 1980. Flora of Panama, Part IX, Family 179. Rubiaceae. Part I. Ann. Missouri Bot. Gard. 67: 1-255.
ENDLICHER, S. L. 1838. Genera Plantarum. (Rubiaceae, pp. 520-566).
_____. 1841. Enchiridion Botanicum (Rubiaceae, pp. 269-281).
ERDTMAN, G. 1960. The acetolysis method - a revised description. Svensk. Bot. Tidskr. 54: 561-564.
FOSTER, A. S. 1950. Morphology and venation of the leaf in *Quiina acutangula* Ducke. Amer. J. Bot. 37: 159-171.
_____. 1952. Foliar venation in angiosperms from an ontogenetic standpoint. Amer. J. Bot. 39: 752-766.
GAERTNER, C. F. 1806. Supplementum Carpologicae (p. 69, *tab. 192, fig. 3*).
GMELIN, J. F. 1791. Systema Naturae 2: 244.
GOOD, R. 1974. The Geography of the Flowering Plants. ed. 4.
GUILLAUMIN, A. 1932. Contribution to the flora of the New Hebrides. J. Arnold Arbor. 13: 6-7 (*Guettarda*).
HEMSLEY, W. B. 1881. Biologia Centrali-Americana Botany 2: 42.
HICKEY, L. J. 1973. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot. 60: 17-33.
_____. 1979. A revised classification of the architecture of dicotyledonous leaves. *In:* C. R. Metcalfe & L. Chalk (eds.), Anatomy of the Dicotyledons (ed. 2) 1: 25-39.
HOLMGREN, P. K., N. H. HOLMGREN, & L. C. BARNETT. 1990. Index Herbariorum, Part I (ed. 8). Regnum Veg. 120.
HOOKER, J. D. 1873. Rubiaceae. *In:* G. Bentham & J. D. Hooker, Genera Plantarum 2: 7-151.
HOWARD, R. A. 1962. The vascular structure of the petiole as a taxonomic character. Proc. 15th Int. Hort. Cong., Nice 1958 (pp. 7-13).
_____. 1979. The petiole. *In:* C. R. Metcalfe & L. Chalk (eds.), Anatomy of the Dicotyledons (ed. 2) 1: 88-96.
JACOBS, M. 1966. On domatia - the viewpoints and some facts. Proc. Kon. Ned. Acad. Wetensch. ser. C 69: 1-43.
JANSEN, M. E. 1984. A synopsis of Guettardella Benth. and the Old World species of Antirhea A. L. de Jussieu (Rubiaceae: Guettardeae). Blumea 29: 565-588.
JUSSIEU, A. L. DE. 1789. Genera Plantarum. (Rubiaceae, pp. 196-210).
_____. 1791. Ibid. (ed. 2). (Rubiaceae, pp. 218-233.)
_____. 1820. Sur la famille des plantes Rubiacées. Mém. Mus. Hist. Nat. Paris. 6: 365-409.
LINDLEY, J. 1846. The Vegetable Kingdom. (Cinchonaceae, pp. 761-765).
_____. 1847. Ibid. (ed. 2). (Cinchonaceae, pp. 761-765).
_____. 1853. Ibid. (ed. 3). (Cinchonaceae, pp. 761-765b).
MELVILLE, R. 1976. The terminology of leaf architecture. Taxon 25: 549-561.
MERRILL, E. D. 1923. An Enumeration of Philippine Flowering Plants. Vol. 3. (Rubiaceae, 492-576).
NICOLSON, D. A. 1979. Neolaugeria, a new name for Terebraria (Rubiaceae) of the West Indies. Brittonia 31: 119-124.
O'BRIEN, T. P. & I. VON TEICHMAN. 1974. Autoclaving as an aid in the clearing of plant specimens. Stain Tech. 49: 175-176.
PIJL, L. VAN DER. 1969. Principles of Dispersal in Higher Plants.
PRAY, T. R. 1953. Morphological and Histogenetic Studies on the Foliar Venation of Certain Angiosperms. Thesis, University of California, Berkeley. (Rubiaceae, pp. 172-264).
_____. 1959. Pattern and ontogeny of foliar venation of *Bobea elatior* (Rubiaceae). Pacific Sci. 13: 3-13.
RICHARD, A. 1830. Mémoire sur la Famille des Rubiacées.
ROBBRECHT, E. 1988. Tropical woody Rubiaceae. Opera Bot. Belg. 1: 1-271.
SCHUMANN, K. 1891. Rubiaceae. *In:* A. Engler & K. Prantl, Die Natürlichen Pflanzenfamilien IV. 4: 1-156.
SEALY, J. R. 1956. The Roxburgh Flora Indica drawings at Kew. Kew Bull. 1956: 297-399.
SOLADOYE, M. O. 1982. Comparative petiole anatomy as an aid to the classification of the African genus *Baphia* Lodd. (Leguminosae - Papilionoideae - Sophoreae). Bot. J. Linn. Soc. 85: 297-313.
SOLEREDER, H. 1908. Systematic Anatomy of the Dicotyledons. (Rubiaceae, pp. 444-454, 950-952).
STANDLEY, P. C. 1934. Rubiaceae. North American Flora 32: 214-277 (Guettardeae).
STANDLEY, P. C. & L. O. WILLIAMS. 1975. Flora of Guatemala - Rubiaceae. Fieldiana: Botany 24(part XI, nos. 1-3): 1-275.
STEENIS, C. G. G. J. VAN. 1950. Flora Malesiana. Vol. 1.
STEYERMARK, J. A. 1967. Guettardeae. *In:* B. Maguire, Botany of the Guayana Highlands, Part VII. Mem. New York Bot. Gard. 17: 333-341.

_____. 1974. Rubiaceae. Guettardeae. *In:* T. Lasser, Flora de Venezuela 9: 772-867.
Takhtajan, A. L. 1969. Flowering Plants, Origin and Dispersal.
Urban, I. 1899. Species novae, praesertim Portoricensis. Symb. Antil. 1: 435-440 (*Antirhea*).
_____. 1912. Nova genera et species. Ibid. 7: 411-412 (*Antirhea*).
_____. 1915. Sertum Antillanum. I. Fedde Repert. 13: 479-481 (*Antirhea*).
_____. 1923. Plantae Cubenses Ekman. I. Symbolae Antillanae 9: 159-160 (*Antirhea*).
_____. 1928. Plantae Cubenses Ekman. IV. Ibid. 9: 528-530 (*Antirhea*).
_____. 1929. Plantae Haitiensis et Domingensis novae vel rariores VI. Ark. Bot. 22A(10): 93-94 (*Antirhea*).
_____. 1932. Plantae Haitiensis et Domingensis novae vel rariores X. Ibid. 24A(4): 50-53 (*Antirhea*).
Valeton, T. 1909. Beiträge zur Kenntniss der Gattung Timonius. Bull. Dép. Agr. Ind. Néerl. 26: 1-61.
Verdcourt, B. 1958. Remarks on the classification of the Rubiaceae. Bull. Jard. Bot. Brux. 28: 209-281.
_____. 1983. Notes on Mascarene Rubiaceae. Kew Bull. 37: 570-571 (Guettardeae).
Welle, B. J. H. ter, A. A. Loureiro, P. L. B. Lisboa, & J. Koek-Noorman. 1983. Systematic wood anatomy of the tribe Guettardeae (Rubiaceae). Bot. J. Linn. Soc. 87: 13-28.
White, C. T. 1946. The Australian species of Antirhea, and a new name for a Cuban species. J. Arnold Arbor. 27: 121-122.

3 2044 093 361 103